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COMPETITION AND FACILITATION IN ASPEN AGROFORESTS

by

©

George Wilfred Powell

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

Plant Science

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Faculty of Graduate Studies and Research

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Dr. Dale Bartos

Sept. 12, 2003

Thesis approved by committee:

"Things are not what they appear to be, nor are they otherwise."

Attributed to Siddhartha Gautama, the Buddha

Surangama Sutra, 705 CE

ABSTRACT

Developing agroforestry systems in Canada requires an understanding of the ecological processes that influence production. Complementary experiments in northern aspen (*Populus tremuloides* Michx.) agroforests identified mixes of competition and facilitation, with above- and below-ground effects. Facilitated soil moisture and nitrogen increases, and aspen damage reduction were observed in mixtures of aspen seedlings with alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.). However, these effects were often masked by competition for light, water and nitrogen that reduced most aspects of aspen seedling growth. Canopy removal and root trenching in aspen stands in Aspen Parkland and Lower Boreal ecosystems revealed understory microclimates favourable for cool-season plant growth. Aspen cover reduced soil water loss during drought, frosts, air temperatures (T), and increased relative humidity (RH). Trees had less effect on averages than in moderating extremes. Aspen also competitively reduced photosynthetically active radiation (PAR) and soil water. With the exception of PAR, there were few season-long microclimate differences between partial and full canopies. Understory production and composition responded strongly to canopy removal with less consistent results from trenching. When trenching was significant, it generally coincided with increased PAR resulting from canopy removal. This interaction was particularly strong among grasses. Production under a partial Parkland canopy was comparable to that with complete canopy removal and demonstrated balanced competition and facilitation. Experiments on alfalfa quantified specific physiological and production responses in an aspen understory. In growth chambers, RH had a small, positive effect on alfalfa growth, particularly when in conjunction with greater PAR. In the field, alfalfa leaf-to-atmosphere vapour pressure difference (D) decreased with aspen cover. Alfalfa leaf T and D were strongly coupled to air T, with RH having a smaller effect. Direct PAR received also influenced leaf T, with shaded leaf T less than or equal to air T, and illuminated leaf T greater than air T. These results collectively support general theories on the importance of facilitation: facilitation mitigated intermittent extremes, but was otherwise masked by persistent competition. Balancing facilitation and competition in agroforestry design is possible through further elucidation of the appropriate level of aspen cover.

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LIST OF SYMBOLS AND ABBREVIATIONS

ACR	above-ground competitive response
APL	area per leaf
AH	absolute humidity
AHD	absolute humidity difference
ANOVA	analysis of variance
BA	basal area
BAI	basal area increment
BCR	below-ground competitive response
°C	degrees Celcius
C3 plant	plants exclusively utilizing the Calvin photosynthetic pathway
C4 plant	plants utilizing PEP carboxylase in addition to the Calvin photosynthetic pathway.
Ca	calcium
cm	centimeter
CO_2	carbon dioxide
d	day
D	leaf-to-atmosphere vapour pressure difference
g	gram
ha	hectare
K	potassium
KCl	potassium chloride
kg	kilogram
kPa	kiloPascals
m	meter
meq	milliequivalent
mg	milligram
Mg	magnesium
ml	millilitre
mm	millimeter
N	nitrogen
NH_4-N	ammonium
nm	nanometer
NO_3-N	nitrate
P	phosphorus
PAR	photosynthetically active radiation
ppm	parts per million
QMD	quadratic mean diameter
R:FR	ratio of red to far-red wavelengths
RGR_D	relative diameter growth

$\mathrm{RGR}_{\mathrm{H}}$	relative height growth
RH	relative humidity
RMANOVA	repeated measures analysis of variance
RYT	relative yield total
s	second
SL	stem-to-leaf mass ratio
SLW	specific leaf weight
SM	soil moisture
SML	stem mass-to-length ratio
SR	shoot-to-root mass ratio
T	temperature
TCR	total competitive response
TEC	tree-environment-crop interaction
yr	year
β	Type II error
µm	micrometer
µmol	micromole

CHAPTER 1

Introduction

1.1 Rationale for Agroforestry

Agroforestry is the concurrent production of trees, or other perennial woody crops, with herbaceous crops, and/or livestock on the same unit of land (Nair 1985). Agroforestry is a common land management practice in tropical and subtropical areas where population pressures have dictated the co-evolution of efficient land use (through better resource capture) and natural resource conservation (Wojtkowski 1998). These same factors are creating interest in developing and applying agroforestry practices in temperate areas, although they are being adopted more slowly in North America.

The potential for increased land productivity, resource conservation, and forest product market developments all give impetus for the adoption of agroforestry systems in north temperate and boreal regions of Canada. Increasing demand for poplar and aspen (*Populus* spp.) for the production of pulp, veneer and composite structural wood products has generated interest in their cultivation on farmland (Balatinecz *et al.* 2001, Ondro 1991, Ward 2001). Indeed, demand for trembling aspen (*Populus tremuloides* Michx.) increased tenfold in Alberta during the 1980s (Ondro 1991) and has continued to date as more forest processing facilities have begun production across the Canadian Prairie Provinces. At the same time, agricultural activities continue to expand and compete for production on the same land base (Fitzsimmons 2002, McCartney 1993, Ramankutty and Foley 1999). The simultaneous rise in demand for land capable of agricultural and forest production provides an opportunity for integrated use through the development of both extensive and intensive agroforestry systems.

Extensive agroforestry systems are those that require few external inputs, and are conducted over relatively large areas. In Canada, this is almost exclusively forest grazing (silvopastoral systems) conducted on public land. Rapid expansion of timber harvesting in the boreal forests (Ondro 1991) has greatly increased the area occupied by regenerating aspen stands in the last two decades. By law, these areas must be returned to productive forest cover after harvest (Alberta Land and Forest Services 1996). The continuation or expansion of grazing on public forestland, therefore, dictates compatibility of range management practices with forest regeneration. Given this potential overlap and conflict in land use, agroforestry systems offer a solution that accommodates both land uses.

Intensive agroforestry systems are distinguished by relatively greater inputs on smaller areas of primarily private land. Suitable intensive agroforestry systems for the northern temperate and boreal regions include livestock production with traditional or short-rotation woodlots (silvopastoral systems) or production of crops between widely spaced tree rows, with or without livestock production (agrisilvicultural and agrosilvopastoral systems).

Due to their rapid growth, ease of propagation, and variety of useful end products, poplar trees have been cultivated in conjunction with other agricultural activities since pre-history (Gordon 2001). Aspen and other poplars are suitable for agroforestry production on the northern Canadian prairies and boreal areas. Trees of the *Populus* genus are the dominant tree species on 20 M ha of forestland in Canada, 71.5% of which is in boreal ecosystems (Peterson and Peterson 1992). Moreover, 29 M ha in the Boreal Mixedwood ecotype naturally supports some aspen cover (Strong and Leggat 1992). Furthermore, most of the private land in northern Alberta that has not been converted to crop production continues to support aspen stands (Westworth and Associates 1994). Land already cleared for agricultural production can also be afforested with aspen as a means of diversifying farm production. Forest product manufacturers currently obtain a small but growing proportion of their aspen and poplar supply from private land (Ward 2001, Westworth and Associates 1994). With continued growth in demand for hardwoods, coupled with the full allocation of the public aspen forest resource predicted to occur early in this century (Ondro 1991), it is reasonable to expect increased future demand for aspen from private sources.

Aspen woodlots are a viable alternative to marginal agricultural production in the boreal zone (Massie *et al.* 1990, Westworth and Associates 1994). Although the economics of agroforestry options have not been formally evaluated for Canada, they could theoretically also be a profitable long-term venture. Westworth and Associates (1994) concluded the most profitable short-term strategy for aspen woodlots was to maximize the annual harvest rate until all trees were removed. This approach is not suitable for long-term management because of an approximately 30 to 50-yr period with no annual cash flow during the ensuing period of forest regeneration. Moreover, most of the income from the subsequent timber crop is generated from mature timber sales many years after establishment costs are incurred, requiring profits to be discounted for the decreasing buying power of money over that time (Sharrow and Fletcher 1995). Even with the potential to reduce timber-crop rotations through thinning (Bella and Yang 1991) or rapid-growth aspen hybrids (e.g. *Populus tremuloides* X *P. tremula*) (Food and Agriculture Organization 1979), economic discounting may make a woodlot operation unprofitable. By providing annual returns from crops or livestock, agroforestry systems generate cash flow to offset the discount rate of timber production (Sharrow and Fletcher 1995).

Sustained tree cover on agricultural land has also demonstrated benefits as a low-cost method for soil and water conservation (Young 1989), as well as providing wildlife habitat (Wojtkowski 1998). Moreover, trees function as a "carbon sink" and thus, agroforestry systems may contribute to meeting national and international agreements for the reduction of "greenhouse gas" emissions. With the expected implementation of the Kyoto Protocol, producers may be eligible for carbon credit payments from corporate or government entities, further diversifying their income sources.

1.2 Need for Understanding Ecological Processes

Agroforestry systems incorporate the concurrent production of multiple crops with varying growth forms, one of which is a woody perennial. These systems are better able to optimize biological outputs, and therefore differ fundamentally from either conventional forestry or intensive agriculture, which both typically seek to maximize the production of only one component (Wojtkowski 1998). Optimal production in species mixtures can be achieved by physically or temporally separating resource use among components (Cannell and Grace 1993, Scholes and Archer 1997), by encouraging facilitative rather than competitive effects, or a combination of both (Buck 1986). Sharing available resources, by separating their use in space and time, potentially allows for greater overall production in mixtures than through monocultures of either trees or understory crops (Buck 1986, Man and Lieffers 1999, Wojtkowski 1998). Studies in temperate systems, however, have only provided limited confirmation that mixtures of tree and herbaceous crops can be more productive than equivalent combined areas in monocultures of both (Bailey and Gupta 1973, Sharrow *et al.* 1996).

Understanding the ecological processes and key interactions in herbaceous and woody plant mixtures (resource capture, resource partitioning, competition and facilitation) would provide a logical basis for the design and development of efficient agroforestry systems. A better understanding of these processes will ultimately assist in identifying the functions and structures that resource managers can manipulate in order to optimize returns from an agroforestry system, while retaining other values and ecological services.

1.3 Theoretical and Experimental Approach

Interactions between aspen and herbaceous vegetation can vary temporally and spatially, and are influenced by management practices. These can include both competitive and facilitative processes, leading to variation in the net effects expressed. Six complementary experiments were conducted to address the variety of potential ecological interactions between aspen stands and their understory, and to isolate and quantify the mechanisms of competition and facilitation. These experiments were used for a preliminary assessment of the agroforestry potential in north temperate and boreal areas in Canada.

Two experiments were conducted in mixtures of aspen seedlings and herbaceous species to assess competition and facilitation during the establishment of an aspen agroforest:

1. Competition and Facilitation in Mixtures of Aspen Seedlings, Alfalfa and Marsh Reedgrass (Chapter 3); and,
2. Root and Shoot Effects in Mixtures of Aspen Seedlings, Alfalfa and Marsh Reedgrass (Chapter 4);

Small plot, field studies employing a fixed-density, species replacement study design were employed to determine the relative competitive ability of aspen seedlings and herbaceous species, and to identify facilitative processes. The first experiment assessed how plant growth and yields were influenced by the relative proportions of each species. The second experiment selectively removed above- and below-ground effects between aspen seedlings and the herbaceous species by means of root exclusion tubes to separate root contact, and netting to separate canopy overlap.

A separate field experiment assessed the dominance of above- or below-ground processes affecting understory dynamics in juvenile aspen stands. This experiment was designed to assess:

3. Effects of Aspen Canopy Removal and Root Trenching on Understory Microenvironment and Soil Resources (Chapter 5); and,
4. Effects of Aspen Canopy Removal and Root Trenching On Understory Species Composition and Production (Chapter 6).

These experiments selectively removed aspen overstory (by cutting out aspen stems) and root interactions (through root trenching) at field sites in the Aspen Parkland and Lower Boreal natural regions of central Alberta. Understory microclimate, species composition, above-ground net primary production and soil parameters were monitored.

Two experiments examined the relative contributions of a main competitive (light reduction) and facilitative (increased humidity) condition associated with the microclimate of mature aspen on the growth and yield of alfalfa (*Medicago sativa* L.):

5. Effects of a Simulated Aspen Understory Microclimate On Alfalfa Growth (Chapter 7); and,
6. Effects of Boreal Aspen on Alfalfa Leaf-to-Atmosphere Vapour Pressure Differences (Chapter 8).

The first of these experiments utilized controlled-environment growth chambers to simulate conditions present under aspen. The second experiment utilized field measures of alfalfa under different levels of aspen canopy to isolate the effects of temperature and humidity on the leaf-to-atmosphere vapour pressure differences.

In combination, these experiments provide an overview and scientific evaluation of the mechanisms, relative strengths and types of interactions between aspen and their understory vegetation. The general principles established from these experiments and implications for agroforestry system design suitable for the Canadian Prairie Provinces are discussed in Chapter 9.

1.4 Literature Cited

Alberta Land and Forest Services. 1996. The Status of Alberta's Timber Supply. Alberta Environmental Protection, Alberta Land and Forest Services, Government of Alberta, Edmonton, AB, 26 p.

Bailey, A.W. and R.K. Gupta. 1973. Grass – woody plant relationships. Canadian Journal of Plant Science 53: 671-676.

Balatinecz, J.J., D.E. Kretschmann and A. Leclercq. 2001. Achievements in the utilization of poplar wood – guideposts for the future. The Forestry Chronicle 77: 217-392.

Bella, I.E. and R.C. Yang. 1991. Should we thin young aspen stands? Pages 135-139 *in*: S. Navratil and P.B. Chapman (editors). Aspen Management for the 21st century: Proceedings of the Symposium, November 20-21, 1990, Edmonton, Alberta. Forestry Canada, Northwest Region, Northern Forestry Centre and Poplar Council of Canada, Edmonton, AB, 174 p.

Buck, M.G. 1986. Concepts of resource sharing in agroforestry. Agroforestry Systems 4: 191-203.

Cannell, M.G.R. and J. Grace. 1993. Competition for light: detection, measurement and quantification. Canadian Journal of Forest Research 23: 1969-1979.

Fitzsimmons, M. 2002. Estimated rates of deforestation in two boreal landscapes in central Saskatchewan, Canada. Canadian Journal of Forest Research 32: 843-851.

Food and Agriculture Organization. 1979. Poplars and willows in wood production and land use. Food and Agriculture Organization Forestry Series No. 10, International Poplar Commission, United Nations Food and Agriculture Organization, Rome, 328 p.

Gordon, J.C. 2001. Poplars: trees of the people, trees of the future. The Forestry Chronicle 77:217-392.

Man, R. and V.J. Lieffers. 1999. Are mixtures of aspen and white spruce more productive than single species stands? The Forestry Chronicle 75: 505-513.

Massie, M.R.C., E.B. Peterson and R.D. Kabzems. 1990. An economic strategy for managing aspen on private lands in northeast British Columbia. Forestry Canada, Canada-British Columbia Forest Resource Development Agreement Report 124, Victoria, BC, 51 p.

McCartney, D.H. 1993. History of grazing research in the Aspen Parkland. Canadian Journal of Animal Science 73: 749-763.

Nair, P.K.R. 1985. Classification of agroforestry systems. Agroforestry Systems 3: 97-128.

Ondro, W.J. 1991. Present and future prospects for poplar utilization in Alberta. The Forestry Chronicle 67: 271-274.

Peterson, E.B. and N.M. Peterson. 1992. Ecology, management, and use of aspen and balsam poplar in the Prairie Provinces, Canada. Special Report 1, Forestry Canada, Northwest Region, Northern Forestry Centre, Edmonton, AB, 110 p.

Ramankutty, N. and J.A. Foley. 1999. Estimating historical changes in land cover: North American croplands 1850 to 1992. Global Ecology and Biogeography 8: 381-396.

Scholes, R.J. and S.R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecological Systems 28: 517-544.

Sharrow, S.H., D.H. Carlson, W.H. Emmingham and D. Lavender. 1996. Productivity of two Douglas-fir/subterranean clover/sheep agroforests compared to pasture and forest monocultures. Agroforestry Systems 34: 305-313.

Sharrow, S.H. and R.A. Fletcher. 1995. Trees and pastures: 40 years of agrosilvopastoral experience in Western Oregon. *In*: Reitveld, A. (Technical Coordinator). Agroforestry and Sustainable Systems: Symposium Proceedings. General Technical Report RM-261, USDA, Forest Service, Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO, pp 47-52.

Strong, W.L. and K.R. Leggat. 1992. Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife, Edmonton, AB, 59 p.

Ward, B. 2001. Poplar as a crop – Its place in a changing agriculture. *In:* Schroeder, W. and J. Kort (editors). Temperate Agroforestry: Adaptive and Mitigative Roles in a Changing Physical and Socio-Economic Climate. Proceedings of the seventh biennial conference on agroforestry in North America, August 13-15, 2001, Regina, Saskatchewan, pp 9 –11.

Westworth, D.A. and Associates. 1994. Aspen woodlot feasibility study. Publication Number I/529, Canada – Alberta Partnership Agreement in Forestry, Edmonton, AB, 113 p.

Wojtkowski, P. 1998. The Theory and Practice of Agroforestry Design. Science Publishers Inc., Enfield, NH, 282 p.

Young, A. 1989. Experimental evidence. Chapter 5 *in:* Agroforestry for Soil Conservation. CAB International and International Council for Research in Agroforestry, Exeter, UK, pp 53-58.

CHAPTER 2

Review of Ecological Processes in Agroforestry Systems

2.0 Introduction

Integrating aspen (*Populus tremuloides* Michx.) production with understory crops in agroforestry systems requires an understanding of the ecological processes that influence the growth and yield of both trees and herbaceous components. This chapter reviews and synthesizes published information on the main ecological interactions pertinent to agroforestry systems. This review is used to identify new information needed for the successful development of agroforestry systems utilizing aspen for north temperate and boreal regions of Canada.

2.1 Overstory - Understory Effects

Established agroforestry systems are generally comprised of woody perennials forming a dominant overstory layer with an herbaceous understory. Agroforestry systems are therefore regulated by overstory-understory relationships. These relationships fundamentally consist of either direct partitioning of abiotic resources (light, water and nutrients) or indirect interactions through modifications of the microclimate. Resource partitioning between the overstory and understory varies with the vertical (canopy layers, rooting profiles) and horizontal (distance, direction) configurations of the ecosystem components (Bergez *et al.* 1999, Sharrow 1991). Moreover, interactions among different species can involve both competitive (resource use or modification by one species diminishes the performance or fitness of another) and facilitative (direct or indirect modifications by one species benefits the performance or fitness of another) processes (Callaway and Walker 1997). Overstory-understory interactions can also vary temporally. That is, they can be facilitative or competitive depending on the plant's developmental stage, the time of year, and even diurnally (Callaway and Walker 1997). As itemized by Sharrow (1991), there are three distinct phases of interactions in agroforestry systems, defined by the growth and development of the woody perennial:

1. *herbaceous phase* - immature trees use few site resources and are subject to strong, direct competition for all resources with herbaceous vegetation;
2. *intermediate phase* - interspecific competition between the understory vegetation and established trees is generally limited to soil-based resources; and,
3. *arboreal phase* - trees control the availability of most resources and intraspecific competition among the trees predominates.

In theory, sharing resources by separating their use either in space and time allows for greater overall production in mixtures than the equivalent combined areas in monocultures of either trees or understory crops (Buck 1986, Wojtkowski 1998). Studies in temperate systems however, have only provided limited confirmation for this theory (Bailey and Gupta 1973, Sharrow *et al.* 1996).

2.1.1 Above-ground Effects

In the herbaceous phase of an agroforest, codominant tree seedlings and herbaceous vegetation interact symmetrically (proportionate to their size). In established agroforestry systems (intermediate or arboreal phases) trees, by virtue of their size and superior canopy position, are the dominant above-ground structural elements and strongly influence resource availability and microclimate in the understory. Tree canopies reduce insolation, precipitation and airflow (wind) to the understory (Brenner 1996). Singularly or in combination, these modifications are responsible for several potential above-ground environmental differences in the understory in comparison to conditions in the open:

1. reduced photosynthetically active radiation (PAR);
2. modified spectral quality of light for plant growth as expressed by the red to far-red wavelength ratio (R:FR);
3. reduced air temperature (T);
4. reduced evaporation from the soil;
5. increased humidity; and,
6. reduced radiative frosts.

Light

The photosynthetically active portion of light is one of the primary resources controlling plant growth. As reviewed by Cannell and Grace (1993) and Montieth (1977), several empirical models relate plant growth linearly to PAR interception. Within plant mixtures, each plant intercepts light in proportion to its share of total leaf area. Moreover, in mixtures with different canopy layers, competition for light is strongly asymmetric, with light reaching any given lower strata according to an application of the Beers-Lambert Law (Equation 1, Salisbury and Ross 1992).

Equation 1. Beers-Lambert Law

$$I = I_0 e^{-KL}$$

where,

I = light penetrating the canopy;
I_0 = light flux density at the top of the canopy;
K = canopy light extinction coefficient; and,
L = leaf area index of the canopy.

Many experiments have shown a negative correlation between understory production and either tree canopy cover, leaf area, or crown volume (Anderson *et al.* 1969, Clary 1969, Ehrenreich and Crosby 1960, Halls and Schuster 1965, Huffman *et al.* 1999, Johnson *et al.* 1986, McKenzie *et al.* 2000, McPherson and Wright 1990, Mitchell and Bartling 1991, Nemati and Goetz 1995, Peek *et al.* 2001, Percival and Knowles 1988, Sharrow *et al.* 1996), or a surrogate for a tree's ability to intercept light, such as stand density or basal area (BA) (Blair and Enghardt 1976, Clary 1969, Ffolliot 1983, Grelen and Lohrey 1978, Halls and Suman 1954, Moore and Deiter 1992, Tapia *et al.* 1990, Tappe *et al.* 1992, Wolters 1973, Wolters 1982). It is important to note however, that although conducted in a variety of vegetation types and habitats, the majority of these relationships were developed for coniferous canopies.

Rowe (1956) concluded light was the principle factor controlling understory production differences in boreal forests based on the pattern of increased light penetration through forest canopies with high proportions of aspen and poplar (*Populus* spp.) corresponding to increased cover of shrubs and herbaceous vegetation. Indeed, Lieffers and Stadt (1993) confirmed a strong relationship between light transmission and boreal tree species; aspen-dominated stands transmitted 14-40 % of available light to the understory, while white spruce (*Picea glauca* (Moench) Voss) dominated stands transmitted only 5-11% of available light.

Light Quality

Plant growth depends not only on the quantity of PAR, but also its spectral composition. Light quality is often expressed as the ratio of light in the red wavelengths (655-665 nm) to that in the far-red wavelengths (725-735 nm) because of the important effect of this ratio on phytochrome balances and resulting hormonal changes in plants (Salisbury and Ross 1992). Live foliage selectively filters more red than far-red wavelengths resulting in a decreased R:FR ratio (Messier 1996, Ross *et al.* 1986). This effect is compounded in a forest understory by a positive linear relationship ($r^2=0.77$, $p<0.01$) between the total amount of light transmitted and R:FR (Ross *et al.* 1986).

Light Thresholds

For a given species, plant growth has both upper and lower thresholds in response to light; that is, photosynthesis responds to a range of light levels, above and below which there is little change. At light saturation, additional units of PAR do not increase photosynthetic activity, whereas at the light compensation point, light levels are insufficient to generate photosynthetic activity in excess of the base respiration needs of the plant. Studies have identified threshold relationships between understory growth and light transmission and its surrogates. Lieffers and Stadt (1993) found the growth of marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) and fireweed (*Epilobium angustifolium* L.) under boreal forest canopies were reduced in comparison to the open with less than 40% of available light and were eliminated with less than 10% of available light. Growth of both species declined linearly with decreasing light levels between these thresholds. Woods *et al.* (1982) noted that herbaceous understory production varied considerably under aspen stands with less than 10 $m^2 ha^{-1}$ BA. Aspen stands with BA between 10 and 18.9 $m^2 ha^{-1}$ however, had less variable production but at much lower levels. In coastal Oregon, subterranean clover (*Trifolium subterraneum* L.) production did not decline significantly until Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) canopy cover exceeded 35% (Sharrow *et al.* 1996). Similarly, Pieper (1990) found the decline in understory production in relation to pinyon pine (*Pinus edulis* Engelm.) was much stronger between canopy covers of 0 and 40%, than under canopies with greater than 40% cover. Likewise, most of the decrease in understory herbage under a mixed oak (*Quercus* spp.) canopy occurred when tree-crown cover exceeded 50% (Ehrenreich and Crosby 1960).

Aspen Stands And Light

The Beers-Lambert law expresses that the nature of the tree canopy (the light extinction coefficient, K) is of equal importance as the leaf area in determining light penetration to the understory. Given the nature of aspen canopies, there are several reasons why aspen stands can transmit more light through their canopy than coniferous species:

1. aspen foliage is less densely arranged than the tightly-bundled fascicles of conifer needles (Landsburg 1986);
2. aspen leaves reflect and transmit more light than conifer leaves and therefore provide more diffuse radiation to the understory (Messier 1996);
3. almost constant leaf movement (from which the common name trembling aspen is derived) produces temporary canopy gaps that allow sun flecks to reach the understory (Roden and Pearcy 1993); and,
4. aspen are deciduous, allowing greater seasonal light penetration in spring and fall when they are leafless (Constabel and Lieffers 1996) but while understory growth is still possible (Landhäusser *et al.* 1997).

Hence, aspen stands need not closely follow the light limiting models developed for determining the effects of conifers on understory production. For example, while herbage production under aspen has demonstrated a negative correlation with aspen BA (Woods *et al.* 1982), other research has found no relationship between aspen overstory and its understory production (Severson 1982, Warner 1971). Indeed, Severson and

Kranz (1976) found no strong relationship between understory production and aspen BA ($r^2 < 0.30$), however, they did find declines in understory production ($r^2 = 0.87$ to 0.95) when the proportion of ponderosa pine (*Pinus ponderosa* Laws.) increased in mixed aspen-pine stands.

Maximum light interception by aspen stands therefore appears to be less limiting to understory growth than coniferous tree species of equivalent total leaf area. This, coupled with the fact that most north temperate and boreal plant species have relatively low light saturation levels, means that light transmission through an aspen canopy may provide nearer the optimal PAR levels needed for understory growth. Observational and empirical studies support this theory. Rowe (1956) noted that boreal aspen stands support a more productive understory compared to mixed or coniferous stands. These observations were confirmed and quantified by subsequent research (Ellis 1986, Genoway 1999, Swan and Dix 1966).

Temperature and Humidity

Trees can have important influences on the energy balance and water relations in the understory through modifications of air temperature and humidity (Brenner 1996). Under warm, dry atmospheric conditions, combinations of high leaf T and low atmospheric humidity result in a high leaf-to-atmosphere vapour pressure difference (D). A large D creates a strong gradient for the movement of water from a plant to the atmosphere and can result in desiccation or xylem cavitation. As a survival mechanism, a large D initiates leaf stomate closure to conserve water by slowing or stopping transpiration, which simultaneously restricts or temporarily suspends photosynthetic gas exchange in plants utilizing the 'C3' photosynthetic pathway (Dang *et al.* 1997). Photosynthesis in warm season or 'C4' plants are also affected by stomate closure, although they are able to continue fixing carbon under lower carbon dioxide (CO_2) and higher oxygen partial pressures, and thus can continue photosynthesis longer with D induced stomate closure. Moreover, the first enzyme catalyzing photosynthesis in C3 plants (rubisco) rapidly loses its affinity for CO_2 with increasing leaf T. As a consequence, C3 plant species grow best under cool, humid conditions, and are commonly referred to as 'cool-season' plants.

There is a positive association of C3 plant production with shelter from a tree canopy in subtropical to tropical savannas and arid temperate ecosystems. For example, Schott and Pieper (1985) found that while shading from one-seed juniper (*Juniperus monosperma* (Engelm.) Sarg.) was negatively correlated with warm-season grass production, it was positively correlated with the cover of the cool-season, pinyon ricegrass (*Piptochaetiium fimbriatum* (H.B.K.) Hitchc.). Similarly, a negative correlation ($r^2=0.93$, $p<0.01$) best fit the relationship between pinyon pine canopy cover and total understory biomass (including warm season plants), but a positive correlation ($r^2=0.52$ to 0.64, $p<0.01$) of the same canopy was associated with the production of two cool-season grasses (Pieper 1990). Likewise, changes in cool-season grass production compensated for decreases in warm-season grass with increasing Huisache (*Acacia farnesiana* (L.) Willd.) until shrub canopy cover exceeded 32%, after which all understory production declined incrementally with overstory increases (Scifres *et al.* 1982). Finally, Clary and Morrison (1973) observed four to five times greater spring forage production (with a large component of C3 plants) under the crowns of alligator juniper (*Juniperus deppeana* Steud.) than in open areas.

Although net facilitation through reduced T and/or increased humidity is more likely expressed in hot, dry biomes, these processes also occur in temperate and boreal systems. For example, a model validated with limited field data predicted that daily carbon gain in heart-leaf arnica (*Arnica cordifolia* L.) in montane sites could be maximized with early morning and late afternoon sun, and shading during the middle of the day (Young and Smith 1982). The model predicted that the additional transpiration-stress induced from long intervals of sunlight would outweigh the benefits of increased midday PAR. This model is supported by growth patterns of a similar subalpine species, mountain arnica (*Arnica latifolia* Bong.) which demonstrated a 37% carbon gain and an 84% reduction in transpiration under cloud cover and 30% lower daily PAR compared to clear days (Young and Smith 1983). This change translated to a seven fold increase in water use efficiency. Moreover, these gains occurred despite leaf T that was below optimal for photosynthesis. Similarly, Marsden *et al.* (1996) reported stomatal conductance and net assimilation in white spruce were twice as high under a lower leaf-to-atmosphere absolute humidity difference (AHD). Field measures confirmed that spruce seedlings under full and partial aspen canopies experienced a lower AHD than those in openings. Likewise, beaked hazelnut (*Corylus cornuta* Marsh.) daytime stomatal conductance was inversely related to D (r^2=0.45) when D>0.5 kPa even in the presence of moist soils (Hogg *et al.* 2000). On sunny days with a high ambient D (max. 2.3 kPa) there were significant declines in photosynthesis, although differences in daily carbon assimilation were attributed to differences in solar input rather than D.

Cold temperatures can also suppress understory growth and are an important factor for production in northern ecosystems. Trees can have a moderating influence on the radiative balance in cold climates through the emission of long-wave radiation. Although not photosynthetic, long-wave radiation reduces the incidence of radiative frosts and thereby extends the growing season in the understory by reducing or eliminating late spring or early fall frost damage. For example, while spruce seedlings in the open and under aspen had similar photosynthetic rates in the summer, there was a decrease in photosynthetic parameters in the open in spring and fall attributed to increased frost (Man and Lieffers 1997).

Soil Properties

The influence of a tree overstory on soil properties, as separate from their root action on the same (see section 2.1.2) can be simplified as the influence on soil:

1. moisture;
2. temperature; and,
3. nutrients.

Tree canopies can affect the understory soil moisture balance both positively and negatively. Canopies reduce soil moisture by intercepting precipitation and channeling it towards the tree bole. In fact, small precipitation events may be entirely intercepted (Anderson *et al.* 1969). Precipitation reaching the understory can be strongly related to overstory cover and have a direct influence on understory production. For example, Anderson *et al.* (1969) found production under coniferous canopies was better correlated with through-fall precipitation (r^2=0.69, p<0.01) than to light penetration (r^2=0.48, p<0.01). Similarly, Grelen and Lohrey (1978) found herbage yields were more strongly influenced by growing season precipitation (r^2=0.89, p<0.05) than increasing BA (r^2=0.20, p<0.05) of longleaf pine (*Pinus palustrus* Mill.), the latter of which is positively correlated to canopy closure and light interception.

An overstory can also enhance soil moisture through reduced evaporation resulting from lowered understory T and air flow (Smith 2000). Direct measures of reduced evaporation from the soil under tree canopies are common in ecosystems where potential evapotranspiration exceeds precipitation in the open. No net increase may be expected in environments which have inherently low evaporative potential or extremely high precipitation, such that understory soils are generally near field capacity the majority of the time (Coombs and Grubb 2000). Studies linking evaporation changes to understory production differences are less common. For example, Penaloza *et al.* (1985) found that a Monterey pine (*Pinus radiata* D. Don) overstory increased soil moisture levels in comparison to the open and thereby extended the growing season for subterranean clover. Other evidence is indirect and inferred from understory production in relation to rainfall patterns. For example, peak production of herbaceous species was approximately 500 and 1000 kg ha^{-1} greater under digger pine (*Pinus sabiniana* Dougl.) and blue oak (*Quercus douglassii* Hook. & Arn.) canopies, respectively, than in the open (Frost and McDougald 1989). After two years of drought, production under the pine canopy did not differ from the open, but production under blue oak retained a 100 to 150 kg ha^{-1} net gain over the open. The authors concluded the differences were due to soil moisture retention caused by tree shading.

Lower soil T under tree canopies may also promote understory growth in hot climates. Herbaceous production under the canopies of umbrella thorn (*Acacia tortilis* (Forsk.) Hayne) and baobab (*Adansonia digitata* Linn.) trees increased compared to open grasslands (Belsky *et al.* 1989). Improved production was associated with lower subcanopy soil T that produced a higher microbial biomass and greater mineralized soil nitrogen (N). Wilson (1990) also hypothesized that overstory shading increased soil N mineralization. He found 50% shade (from shade cloth) resulted in a 106% increase in soil nitrate-N, and an associated 36% increase in leaf N concentration and 43% increase in herbage yield compared to plants grown in full sun. Although air T under the shade cloth were not reduced, maximum soil T at 2-cm decreased from 45-50 °C (in the lethal range for many soil organisms) to 30-36 °C.

In boreal ecosystems cold soil T are more likely to restrict plant growth (Bonan and Shugart 1989). The deciduous nature of aspen provides for more rapid warming of the soil in the spring relative to evergreen trees. More snow also accumulates under aspen and this reduces the depth of frost penetration into the soil (through snow's insulation) in comparison to under either pine or spruce (Weitzman and Bay 1963). Moreover, snowmelt under leafless aspen begins earlier than under conifers that retain foliage year-round (Brinkman and Roe 1975). The combined effect of these two phenomena is that soils can thaw more rapidly and permits understory growth earlier under aspen canopies in comparison to coniferous stands.

Soil nutrients are influenced by tree canopy litter fall to the soil surface, along with nutrients released from understory vegetation that dies at canopy closure. Litter accumulation can enhance or hinder understory development depending on its volume and chemical properties. A small amount of litter may reduce evaporation from the soil, making more soil water available to herbaceous species (Smith 2000). Conversely, large amounts of litter can 'smother' and greatly reduce or eliminate understory vegetation. Moreover, allelopathic chemicals released from the breakdown of tree litter may hinder understory growth. Freshly fallen aspen leaves have demonstrated an allelopathic effect on some grass species (Younger *et al.* 1980).

Aspen stem and leaf litter plays a key role in regulating nutrient availability in boreal and north temperate ecosystems. Aspen leaves are high in N, phosphorus (P), potassium (K) and calcium (Ca) relative to other trees; ranking first or second in content among northern Rocky Mountain tree species (Daubenmire 1953). Moreover, while rotting aspen logs only accounted for 5% of ground cover in a boreal Mixedwood stand, they accounted for 32% of the white spruce regeneration (Lieffers *et al.* 1996), indicating a potential linkage between aspen litter and boreal soil fertility. Likewise, understory vegetation litter can strongly influence nutrient cycling in forests. For example, in a 40-yr old aspen stand the understory vegetation produced 19% of the total above-ground litter, but contributed 36% of the litter N, 40% of the litter P, and 59% of the litter K (Perala and Alban 1982). Similarly, Ruark (1990) found that understory vegetation represented 14, 24 and 13% of the available pools of P, K and magnesium (Mg), respectively, in a young aspen forest.

2.1.2 Below-ground Effects

Below-ground effects include root-based modifications by plants of soil moisture, nutrients or other soil properties. Similar to above-ground effects, these interactions can be competitive or facilitative, and vary with the spatial and temporal attributes of the system. As a rule, symmetrical competitive interactions between trees and herbaceous species predominate during the herbaceous phase of stand development (Sharrow 1991). Competitive interference of tree growth and survival diminish with root zone separation as the tree roots both expand to deeper soil profiles and attain a wider horizontal spread. Zinke (1962) hypothesized that in a homogenous abiotic environment the influence of a tree on soil properties would develop uniformly about the tree bole, with the zone of influence proportionate to the tree's projected crown area. Therefore, as trees grow in size, competition for soil resources may become asymmetric or remain symmetric (proportionate to the size of the individual plants), but total resource use is always strongly skewed towards the much larger tree root network.

In addition to competition for water and nutrients, root-based interactions may also include (after Schroth 1999):

1. increased soil N from symbiotic N-fixing associations;
2. nutrient sharing through mycorrhizal associations;
3. changes in soil acidity or other chemical properties;
4. nutrient pumping – tree roots deep in the soil profile translocate nutrients to the upper soil horizons, which become available through leaf litter deposition, root exudates and fine root breakdown;

5. changes in the form of soil nutrients through effects of one species on mineralization and demineralization;
6. increases in water holding capacity from additional organic matter in soil resulting from root exudates and fine root turnover;
7. decreased soil water losses through root interception of run-off or deep drainage; and,
8. hydraulic lift of soil water - similar to nutrient pumping, deeply rooted plants pull water from deep soil profiles and release it in shallow profiles.

It should be noted that although the information that follows is presented in separate categories for presentation purposes, there is strong evidence that movement and uptake of many soil resources are linked (Chapin *et al.* 1987). For example, some plant nutrients move to the plant root system in aqueous solution. Competitive or facilitative changes to soil water therefore, will also affect the supply and delivery of those nutrients. Moreover, the simultaneous effects of changes in soil water, nutrients and other chemical properties can be additive on plant growth and survival.

Soil Nutrients

Soil nutrients can limit plant growth and competition for nutrients can ultimately lead to yield suppression or exclusion of one species by another. Evidence for the influence and importance of understory and overstory vegetation on soil nutrient balances comes from three primary sources: plant removal studies, nutrient addition (fertilizer) studies, and root separation studies.

Plant removal studies in mixtures of trees and herbaceous vegetation are generally conclusive of increased nutrient availability with removal of either overstory or understory vegetation. An increase in soil dissolved ions during the first few years after cutting off a tree stem, the so-called "nutrient flush" or Assart effect, is well documented for many species, including aspen (DeByle 1976). Similarly, removing herbaceous species from around trees can result in improved growth during the herbaceous or intermediate phases of stand development (Nambiar and Sands 1993). For example, Clinton *et al.* (1994) found understory plants reduced the maximum rate of Monterey pine needle growth, levels of N, Ca, and Mg uptake, as well as needle mass and nutrient content. In another study, removing understory pasture species doubled the N uptake by Monterey pine (Clinton and Mead 1993). Changes in nutrient availability may also involve interactions with other processes. For example, less available soil N was found under Monterey pine agroforests than in open pastures because of a combination of increased N use with the presence of trees, and decreased N fixation in treed areas resulting from lower clover composition in the understory (Steele and Percival 1984).

Nutrient addition studies show conflicting results in mixtures of trees and herbaceous vegetation. Among herbaceous species, a review found approximately equal numbers of experiments demonstrating increases and decreases in competition following fertilization of mixtures (Wilson 1988). In a field study, Clinton and Mead (1993) showed N applications had a net benefit during the first growing season for Monterey pine under different levels of competition with domestic forage species, but the majority of the N was taken up by pasture plants. Likewise, although plant productivity has consistently been shown to be limited by mineral nutrient availability in boreal systems (Turkington *et al.* 1998), nutrient addition studies are inconclusive of the benefit of adding limiting nutrients to benefit mixtures of trees and herbaceous vegetation. Steneker (1976) speculated that fertilizer would not improve aspen growth in the boreal because understory vegetation would disproportionately take up the nutrients. His theory is supported by the findings of Nams *et al.* (1993) who showed fertilization of boreal soils benefited herbaceous perennials and deciduous shrubs, but had slight to no effect on evergreen shrubs and trees. Likewise, Ruark (1990) found only a "modest" response of aspen growth to N fertilization. Boreal herbaceous vegetation therefore, may be better adapted to take advantage of increased nutrient availability. In contrast however, Weetman *et al.* (1987) found limited evidence for increased aspen volume with fertilization, indicating aspen have the potential to advantageously use increased nutrients under some conditions.

Mixtures of trees and understory vegetation may make better total use of nutrient pools, which can decrease root-based competition for soil resources. For example, despite a greater total nutrient uptake by Monterey pine seedlings compared to that of orchardgrass (*Dactylis glomerata* L.), the mineralized N and sulphate levels were five and two times higher, respectively in plant mixtures (Davis 1995, Davis and Lang 1991). Pines increased the mineralization of organic matter, increasing the available nutrients, and the mix of pine and forage species increased overall utilization of soil nutrients.

Root separation studies in forests by trenching, with or without soil barriers, have generally demonstrated increased available N with removal of tree or shrub root effects (Coombs and Grubb 2000). However, caution should be employed in interpreting these results because many experiments did not separate the effects of the cessation of root effects after root trenching from the increase in N resulting from decaying severed roots (Coombs and Grubb 2000).

Nitrogen-Fixation

The ability of certain plants in symbiotic association with certain blue-green algae and bacteria to fix atmospheric N is well documented. Legumes with these associations are commonly used by land managers to improve soil N status (Walton 1983). Facilitation of understory growth can also occur with N-fixing tree species (Belsky 1994). Nitrogen fixed in these associations and released into the soil as the root nodules break down has been shown to produce a net benefit to tree N content and growth. For example, Douglas-fir had increased ($p<0.10$) foliar N concentrations when grown with subterranean clover (Carlson *et al.* 1994). Likewise, sycamore (*Platanus occidentalis* L.) seedling growth increased when grown with any one of four herbaceous legumes (Haines *et al.* 1978). Unfortunately the experimental design used could not separate the effects of improved tree growth due to N enrichment from potential reductions in competition resulting from the seeded legumes displacing other vegetation (i.e. a weed suppression effect). Trowbridge and Holl (1992) found both increased needle mass and foliar N concentrations in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) grown with alsike clover (*Trifolium hybridum* L.) than those grown without, but only after four years. Similarly, pines absorbed and translocated N fixed by subterranean clover only after several years of soil N accumulation (Pearson *et al.* 1994) emphasizing the importance of longer-term studies. An understory herb, *Marrubium vulgare*, benefited from the "island of fertility" created by the leguminous shrub *Retama sphaerocarpa* (Pugnaire *et al.* 1996). Herbs in the understory had greater ($p<0.05$) leaf area, specific leaf area, leaf mass, shoot mass, flowers and foliar N than plants grown in the open, with growth correlated to increased organic matter and soil N in the understory.

Soil Water

Research examining competition for soil moisture in the herbaceous and intermediate phases of agroforest development has shown varying outcomes. For example, xylem water potentials of Douglas-fir seedlings were reduced by competition with seeded forages after a month with less than 10 mm of precipitation, but generally had little or no effect under normal precipitation patterns for the area (Eissenstat and Mitchell 1983). Carlson *et al.* (1994) also found no difference in mean xylem water potential of Douglas-fir grown with or without subterranean clover. In juvenile stands of Monterey pine however, understory vegetation reduced the maximum tree stomatal conductance on dry sites in comparison to trees grown without an understory (Miller *et al.* 1998).

Competition for soil water in the arboreal phase is generally conclusive of disproportionate use by the trees (Belsky 1994, Brown and Thompson 1965, Callaway *et al.* 1991, Ellison and Houston 1958, Jose *et al.* 2000, Riegel *et al.* 1992, Ssekabembe *et al.* 1994, Sucoff 1982). This is also supported by a review of forest root competition experiments (Coomes and Grubb 2000); increased soil water is commonly observed after segregating the roots of an overstory species from those in the understory. Evidence of asymmetric water use by aspen relative to its understory was shown with transpiration rates of plant communities with and without an aspen overstory (Johnston 1970). Those under aspen had 38% greater evapotranspiration than the herbaceous community alone. Aspen used a greater portion of soil water through both a higher rate and a longer period of transpiration than the understory species. Indeed, aspen bud-break and flowering occurred while the ground vegetation was still covered in snow.

Competitive effects for soil water may also diminish at the arboreal phase as deeper rooted species make use of lower soil strata. For example, Gyenge *et al.* (2002)

recorded improved predawn xylem water potential in needlegrass (*Stipa speciosa*) under high ponderosa pine cover (500 stems ha^{-1}) in comparison to open-grown plants. Total evapotranspiration from the agroforestry plots was greater than in the open grassland, but most of the soil water use by trees was from the deepest soil layer measured (80-140 cm), thus there was complementary production with needlegrass through spatial separation of soil water use. Limited evidence also suggests that surface competition with herbaceous species may force trees to shift their root allocation to deeper soil profiles (Dawson *et al.* 2001). Thus more complementary rooting patterns in agroforestry systems may develop over time as a result of early competitive interactions with herbaceous species.

Deeply rooted woody species can also improve soil water status in their understory through reducing water loss from the system or through the process of hydraulic lift. For example, surface run-off and deep soil drainage were lower under mixed oak (*Quercus* spp.) cover than with grass alone in an arid Mediterranean savanna (Joffre and Rambal 1993). Water losses from the open equated to 65-100% of potential evapotranspiration, but were only 20-40% under oak cover. Likewise Carlson *et al.* (1994) found greater soil water content at 50-100 cm depth under Douglas-fir grown with subterranean clover than in soils without tree cover. Moreover, Tew (1968) associated greater water holding capacity in soils under aspen than adjacent herb-shrub communities to a 4% greater organic matter content.

Hydraulic lift is the movement of water from roots into soil layers with lower water potential. If roots span a vertical gradient in soil water potentials, then water drawn up from deep profiles and released into shallow soil zones can facilitate plants rooted in the shallow layers. Hydraulic lift has been observed in 27 species, primarily in arid landscapes (Caldwell *et al.* 1998). In wet habitats, water depletion may also be beneficial. Water use by one species can decrease the soil water content enough to facilitate the growth of a less flood-tolerant species (Man and Lieffers 1999).

Other Soil Properties

Overstory and understory species also influence other soil chemical and physical properties. Soil bulk density and acidity generally decrease with increasing distance from conifers (Zinke 1962). This is of particular importance in the boreal zone where soil pH is strongly influenced by type of tree cover, and acidity can restrict plant production. Aspen stands have been associated with a decrease in boreal soil acidity by approximately 0.5 pH unit compared to white spruce or paper birch (*Betula papyrifera* Marsh.) stands (Pare and Bergeron 1996) and a decrease of 0.1 to 0.2 pH units compared to adjacent herb-shrub communities (Tew 1968).

2.2 Separating Competition From Facilitation

Facilitative and competitive mechanisms do not act in isolation of each other and can vary temporally, spatially and at different scales within the same system (Holmgren *et al.* 1997). Depending on the strength of individual processes relative to resource availability and other environmental conditions there are three possible outcomes of plant-to-plant interactions (Scholes and Archer 1997):

1. net competition;
2. net facilitation; or,
3. balanced or neutral effects.

For example, net facilitation of understory plant growth in agroforestry systems can occur when improved water or nutrient supply under the tree canopy is greater than the 'costs' of the lower light levels associated with the overstory. Net competition could occur if the opposite were true. The balance of these processes has important implications for the design of agroforestry systems. Net facilitation or neutral effects are desired; alone or coupled with resource use separation in time or space they can result in 'overyielding.' Overyielding, otherwise known as a positive land use equivalency ratio, occurs where total productivity of mixtures of trees and understory crops produces greater outputs than equivalent areas in monoculture of both (Wojtkowski 1998).

Despite the importance of competitive and facilitative processes to the outcome of plant interactions in agroforestry systems, they have rarely been simultaneously isolated and quantified in agroforestry systems. A notable exception is the mixture of facilitated and suppressed herbaceous growth found in relation to N-fixing umbrella thorn trees (Belsky 1994). Herbaceous production was observed to be greatest under the tree canopy, lowest in the tree's root zone (but not shaded by the canopy), and intermediate in the open grassland without the influence of trees. A combination of artificial shading, fertilizer and root trenching were applied to the three zones to determine the mechanisms responsible for the differences. Net facilitation was expressed in the shaded canopy zone where the improved soil moisture (through reduced evaporation) and nutrients (through N-fixation or mineralization) offset reduced light levels. Net competition was expressed in the unshaded tree-root zone where reduced soil moisture countered the benefits of N fixation and full sunlight.

Simultaneous competition and facilitation of soil water was observed in mixes of mature poplar (*Populus deltoides* Bartr. Ex. Marsh) and forage species. The presence of trees increased total evapotranspiration in a pasture by up to 36% over an open pasture, with the majority of the water use accounted for by tree effects (Guevara-Escobar *et al.* 2000). Surface soil moisture content (0-30 cm) under poplar however, was still greater than the open pasture due to decreased evaporation associated with the trees, indicating soil water use by the trees was compensated for by facilitation through decreased evaporation.

The balance between competitive and facilitative effects may also shift temporally at different stages of plant development (Callaway and Walker 1997). For example, white clover (*Trifolium repens* L.) establishment was positively associated with longleaf and slash pine (*Pinus ellitoii* Engelm.) BA, but the following year, established clover production was negatively related to pine BA, emphasizing the temporal nature of some effects (Halls and Suman 1954).

Competition and Facilitation Along Resource Gradients

The balance between competition and facilitation is also theorized to vary along resource gradients, with net competition expressed with increased resource availability and net facilitation occurring under extremes in environmental conditions or disturbance

(Bertness and Callaway 1994, Brooker and Callaghan 1998, Holmgren *et al.* 1997). These predictions are based in the theories that primary productivity generally intensifies along gradients of decreasing stress (abiotic or disturbance), and competition increases with increasing productivity (Grime 1979). Furthermore, facilitation is believed to be strongest when the environmental variable being ameliorated by one plant for the other is "extreme" (either high or low). Facilitation may always be present, but is believed to be masked by a greater impact of competition in more productive or low disturbance situations.

Limited evidence from field research supports these theories. For example, low rates of N fertilizer produced better results than high rates on very nutrient deficient soils for agroforestry applications (Campbell *et al.* 1994). Competition was maximized with higher rates through tree mortality, which set-back the overall production of the tree-forage system, compared to lower N rates. Moreover, Ratcliff *et al.* (1991) found that peak standing forage crop correlated negatively or positively to resource levels depending on the overstory tree species, topography and range site potentials. Likewise, McClaran and Bartolome (1989) observed that peak herbaceous production under blue oak varied with annual rainfall patterns. Understory production equaled that of the open at sites with less than 50 cm of precipitation per year, but biomass production in the open was greater than under an oak canopy at sites with more than 50 cm of annual precipitation. The authors concluded that understory production benefited from lower evaporation at dry sites, but facilitation was masked by increased competition at high rainfall sites. Belsky (1994) also found that savanna trees compete more intensely with their understory at wetter sites than at dry sites. Finally, Mueggler and Bartos (1977) provide limited evidence for shifts in net facilitation relative to environmental conditions. A 41-yr old montane aspen clear-cut, with regeneration suppressed, produced 60% more forage than an adjacent uncut aspen forest. At a higher elevation site (with a shorter growing season) however, a stand of the same age, and also free from aspen reproduction, produced 25% less forage than its adjacent uncut area. Thus, the presence of an aspen overstory resulted in a net decrease in understory production at the low elevation site, while net facilitation was expressed at the higher elevation.

These theories however, have not been widely tested, nor are the base assumptions and associated hypotheses universally accepted. First, there is no consensus as to whether the intensity or form of competitive interactions increases or remains constant along gradients of resource availability (Taylor *et al.* 1990), nor if there is any reason for a consistent relationship at all (Davis *et al.* 1998). Additionally, facilitation is not always expressed in "harsh" environments (Olofsson *et al.* 1999).

2.3 Determining the Dominance of Above- or Below-ground Effects

In agroforestry systems, it is important to identify and distinguish between forms of plant interactions in order to determine the appropriate system design and management actions. In agroforestry systems, the crop portion of both overstory and understory components is often from the above-ground portion of plants. Changing the balance between understory and overstory resource use in established agroforests can be achieved by reducing the overstory to reduce light interception. However, this also reduces the tree crop and doesn't recognize that competition for water or nutrients coupled with the presence of an overstory may be more responsible for understory yield reductions than reduced light. Indeed, facilitation from overstory effects may offset the impact of reduced PAR, and soil resource deficits can also be mitigated through fertilization or irrigation in some agroforestry settings.

Limiting Resources Theories

As reviewed by Wojtkowski (1998), theories of plant growth in relation to resource availability provide insight into the relative importance of the resource supplies in agroforestry systems. Liebig's 'law of the minimum' predicts that the single growth factor in shortest supply sets an upper limit to plant growth. By Liebig's law, adding additional units of the limiting factor will increase production until it is limited by some other resource. In contrast, Liebscher's 'law of the optimal' hypothesizes that once an upper limit for the most limiting resource is attained, productivity depends on the relative amounts of other resources necessary for growth. The multiple limitation hypothesis (Chapin *et al.* 1987) predicts shifts in plant allocation to root or shoot structures will determine the relative efficiency with which limiting resources are gathered. By this theory, plant fitness is maximized by "optimal foraging," and shifts in root and shoot allocations should shift resource uptake, and thus, make all key resources limit growth simultaneously (Gleeson and Tilman 1992). The theory of resource supply and demand (Davis *et al.* 1998) predicts that what influences individual plant growth is not necessarily a change in gross resource supply or a change in abundance or size of neighbors, but the extent to which resource availability is affected by the balance between supply and demand for the resource. These theories, in particular the concept of resource supply and demand, are implicit in the general tree-environment-crop interaction (TEC) equation (Kho 2000). The TEC equation was developed as a general predictive tool for understanding resource partitioning and use in agroforestry systems (Equation 2). Determining the importance of a particular resource to plant growth in an agroforestry system requires an understanding of how additional units of that resource will alter yield, and how other components in the system affect its availability and uptake.

Equation 2. General Tree-Environment-Crop Equation

$$I = \Sigma\ (L_i T_i)$$

Where,

I = overall impact on understory crop production, defined as the difference in yields produced in an agroforestry system and in monoculture, divided by the yield in monoculture;

L_i = environmental coefficients for the weighted change in availability of light, water, nitrogen, and other nutrients; and,

T_i = net tree effects on the availability of light, water, nitrogen, and other nutrients.

Tree effect coefficients can be positive (net facilitation), negative (net competition) or zero (neutral effects). Kho (2000) demonstrated that environmental coefficients (L_i) can range from 0 (no impact) to 1 (sole environmental factor affecting growth), and their sum for any given system is constant. Thus, if one L-coefficient increases, the sum of the others must decrease. From this model, general predictions can be made of tree-crop interactions. For example, if a resource is not limiting to plant growth (i.e. $L_i = 0$), the overstory effect on an understory crop through its influence on that resource must also be negligible. Conversely, the more limiting a resource is to crop production (as L_i approaches 1) the greater the potential impact of the tree effects (either positively or negatively) will be via that resource. On the basis of the TEC model, two general resource availability rules were developed for agroforestry systems (Kho 2000).

1. The greater the availability of a resource (other factors being equal), the smaller its limitation (L_i) and share ($|L_iT_i|$) of the overall interaction. This rule is analogous to the law of the minimum.
2. The greater the availability of a limiting resource, the greater the effect of the remaining resources to the overall interaction. This rule is analogous to the law of the optimum.

Thus, an understanding of how both trees and environmental factors affect resource availability, can be used to predict the total influence on understory crop production.

Evidence Inferred From Growth Patterns

Experimentally, it is difficult to fully separate the effects of light from the effects on soil-based resources through manipulation of the system. One approach is to remove plants to determine the change in the system in its absence. However, plants with large leaf areas intercept large amounts of light and also use large amounts of water and nutrients. Removing large plants, therefore, simultaneously increases light and also water and nutrient availability, making an unambiguous determination of the dominance of above- or below-ground processes unattainable (Cannell and Grace 1993). An added complication of this approach in forest systems is the large amount of disturbance necessary to remove a tree, with the resulting increase in decomposing organics from the root system.

An approach to solving this dilemma is to infer the dominance from observed patterns of plant forms or growth. The distinct divergence of plant forms (overstory trees with understory herbaceous plants) suggests that asymmetric competition for light determines understory production in agroforests (Cannell and Grace 1993). Adaptations to a low light environment or facilitative effects also resulting from the canopy however, may not make this pattern universally true. For example, production patterns around Douglas-fir trees indicated the dominance of below-ground processes (Harris 1998). Because shade patterns are disproportionately distributed to the north of a tree bole in the northern hemisphere (an anisometric pattern), it was reasoned that if light was the factor most limiting growth, understory production should display the same pattern. Because understory plants showed equivalent production at equivalent distances from the tree bole (an isometric pattern), irrespective of direction, it was concluded that soil resources limited production.

Experimental Separation of Effects

Above and below-ground processes have also been separated experimentally by selectively removing shading or root mixing. This research has produced varied outcomes; however, the majority of experimental evidence suggests that below-ground competition for resources generally controls productivity. For example, root-based competition was the dominant process from a review of 23 greenhouse studies where root and shoot effects were simultaneously separated (Wilson 1988). Likewise, 40 of 47 reviewed root trenching studies in forest ecosystems reported a positive plant response in the species released from overstory root effects (Coombs and Grubb (2000); where there was no response it was generally due to concomitant very low light levels.

Ellison and Houston (1958) found greater forage production under aspen with roots trenched than under either untrenched aspen or in adjacent openings. Their results indicate that aspen root competition limits understory production, and that an aspen overstory with root competition suppressed (through trenching) facilitates understory growth. Unfortunately, their data are confounded because they did not trench plots without an aspen canopy, and thus, those plots were still subject to root competition from shrubs and any lateral aspen roots that may have extended from adjacent forested areas.

Tiedemann and Klemmedson (1977) selectively removed shade (through stem removal) and root action of mesquite (*Prosopsis juliflora* Sw. DC). Artificial shading applied without root competition increased perennial grass production. However, no increase in soil moisture was observed with elimination of root action suggesting the observed increased understory production was due to the facilitative effects of shading.

Understory hardwood tree seedlings showed improved survival associated with increased soil moisture levels after severing the roots of overstory species (Horn 1985). Leaf area and height growth however, were positively correlated to light availability, and these associations were stronger when combined with root trenching. Likewise, root trenching around solitary loblolly pine (*Pinus taeda* L.) increased understory herbaceous plant density, but only increased biomass with the elimination of shade (Monk and Gabrielson 1985). These data suggest both above- and below-ground resource availability can be simultaneously important, but can act on different parameters of understory response.

Callaway *et al.* (1991) reviewed research on California savannas and found conflicting reports of blue oak canopy effects on understory production. Understory production ranged from a 25% decrease of that in the open, to increases of more than 200% greater than in the open. They selected 12 trees that showed a positive relationship between overstory cover and understory production, and 12 trees that showed the opposite. Irradiance was reduced equally (to 45% of open) under the canopies of both groups of trees, and there were also differences in water use and root distributions. Trees having a negative association with understory production showed lower herbaceous xylem pressure potentials, which in turn, were correlated with greater fine tree roots in the upper 50 cm of soil. These results suggest that shading or litterfall was benefiting understory production, but tree root competition for soil moisture was the most important factor determining understory development.

Putz and Canham (1992) found the growth of red maple (*Acer rubrum* L.) and white ash (*Fraxinus americana* L.) seedlings improved on dry, nutrient poor soils with trenching of competing shrub roots, but not with opening the shrub canopy. Riegel *et al.* (1992) found reduction of ponderosa pine root competition (through root trenching to a 1 m depth) increased soil water potential and mineralized N, and decreased soil acidity and understory graminoid xylem water potential. These changes resulted in a 53-94% increase in understory biomass. Reductions of tree density through thinning increased the PAR and air temperature, and decreased the humidity in the understory, but did not improve understory production. The authors concluded that soil-based competition was limiting understory growth in ponderosa pine forests. Belsky (1994) also found evidence of the dominance of root-based interactions under N-fixing umbrella thorn trees in a subtropical African savanna.

Intensity of competition from herbaceous vegetation on the growth and survival of bur oak (Quercus *macrocarpa* Michx.) and northern pin oak (*Q. palustrus* Muenchh.) seedlings increased with declining soil water supply (Davis *et al.* 1998). Growth was reduced by shading as well, however it interacted strongly with soil moisture levels. Survivorship declined in full sun with decreasing water levels, while under shade, the impacts were strongest in dry plots, lowest in intermediate plots, and rising once again with very wet conditions.

Soil water competition was the determining factor in corn (*Zea mays* L.) production between rows of black walnut (*Juglans nigra* L.) in a temperate alley cropping system (Jose *et al.* 2000). Surface soil water levels (0-30 cm) and water uptake by corn increased when the black walnut roots were excluded from the alleys by root barriers. Furthermore, black walnut transpiration increased without the presence of barriers, indicating they were utilizing water from the corn zone. At the same time, trees had little impact on light levels in the alleys, suggesting below-ground competition determined production in these systems.

Soil water competition was also found to be significant in alley crops of corn between rows of 7 yr-old silver maple (*Acer saccharinum* L.) in Missouri (Miller and Pallardy 2001). Soil water content (at 15, 30, 45 and 60-cm), predawn and midday corn xylem water potentials and net photosynthesis in the corn were all lower ($p<0.05$) immediately adjacent to the tree rows in comparison to corn grown in the middle of the alley. No differences in these variables were detected when root trenching with plastic barriers separated tree roots from the corn alleys. Likewise, soil water in trenched, lined plots under a mesquite canopy did not differ ($p=0.59$) from the open (Teague *et al.* 2001), indicating soil moisture levels were determined by root interactions, not the effects of canopy shading.

In an arid zone of Niger, an overstory of Acacia albida (*Faidherbia albida* (Del.) A. Chev.) was found to improve pearl millet (*Pennisetum glaucum* (L)R.Br.) production by 36% in comparison to an open grown crop (Kho *et al.* 2001). By partitioning the variation in growth associated with different interactions of the trees on resource availability, the authors determined that increased N and P in the understory were responsible for 26% and 13% yield increases, respectively, while the combined effects of reduced light and water had a net reduction on yield of only 3%.

Interactions Between Above- and Below-ground Effects

Although traditionally viewed as additive, above- and below-ground effects may interact to produce a total interaction greater or less than simply the sum of these processes in isolation (Cahill 1999). However, Cahill (1999) theorized interactions were not likely in forests or other plant communities with a perennial hierarchy of plant sizes because the understory species would likely be adapted to photosynthesize in low light conditions, and therefore the size differences of the root profiles and canopies would not be compounded. This may not always be the case in agroforestry systems however, where species adapted to greater light conditions may be purposefully cultivated in the understory.

Plants do not compete for light without simultaneously competing for water and nutrients (Cannell and Grace 1993). Plants limited by light availability will experience lower transpiration that can limit their ability to extract soil water and nutrients. For example, rain forest tree seedling growth after root trenching, inside and outside of forest gaps, displayed significant increases in relative growth rates of height and leaf production (Lewis and Tanner 2000). The absolute level of the trenching impact however, depended on the PAR level. Similarly, Coombs and Grubb (2000) concluded from a review of previous research that nutrient additions to forest understory vegetation generally produced a response when irradiance was also in excess of 5% of full sunlight, but generally showed no response with irradiance of less than 2% of full sunlight. Likewise, plants stressed by water or nutrient deficiencies may produce less leaf area, thereby reducing their ability to intercept light. Studies on the effects of fertilizer on boreal vegetation have been conflicting, in part because of the interaction of nutrient supply with light levels (Turkington *et al.* 1998).

Separating above- and below-ground effects under aspen may further be complicated by the clonal nature of this species and below-ground dynamics following stem removal. Cutting aspen stems will restrict photosyntate inputs to the root system to those transferred via the underground clonal network from aspen in adjacent uncut areas. This can result in reduced below-ground competition through fine root die-back. However, Shepperd and Smith (1993) found no declines in aspen roots (greater than 4-mm diameter) in the upper 20-cm of soil, 2 to 6 years following complete canopy removal in montane aspen stands. Moreover, suckering following aspen stem removal appears to have little impact on root numbers or surface area (Shepperd *et al.* 2001).

2.4 Summary and Conclusions

Predicting Specific Outcomes in Agroforestry Systems

Experimental evidence either in favour or against the use of agroforestry systems is extrapolated from a wide variety of systems, but is generally indirect or qualitative (Ong 1996). Production in agroforestry systems is governed by a complex mixture of ecological processes and interactions, and the sheer volume of pertinent ecological theory is daunting. Moreover, temporal variability, resource pulses (Goldberg and Novoplansky 1997) and species or site specific considerations (Cahill 2002) dictate that all these theories are subject to qualifications and exceptions. Interpretations are further complicated by the type of agroforestry system employed. The response in simple agroforestry configurations (one tree species combined with one understory crop) is less complicated than in mixes of trees and complex polycultures of understory vegetation. In complex mixtures (e.g. semi-natural silvopastoral systems), synecological interactions not only influence plant production, but may also change species composition. As evidenced in the preceding sections, above- and below-ground resources, with competitive or facilitative processes, in isolation or when interacting, with direct and indirect effects have all been shown to be either important or unimportant for determining productivity in plant mixtures. Difficulty in interpreting these conflicting results is often compounded by the inconsistent definition of key concepts (e.g. competition, Weldon and Slauson 1986), and the disparate use of experimental methods, which generate information in partial support of several theories, but are unable to make an unambiguous assessment of individual theories.

The theoretical considerations for growing trees with other crops are well established (Kho 2000). These theories provide a general guide from which to explore agroforestry design for Canada, but in no way provide a predictive framework to assess integrated aspen and forage production. Although agroforestry is widely practiced throughout the world, these systems will not be suitable in all situations. There are biophysical limits within which agroforestry systems are advantageous, but also environments in which combinations of trees and other crops are disadvantageous in comparison to conventional forestry and agricultural practices (Ong 1996). Therefore, the specific relationships between aspen and herbaceous species need to be tested under regional conditions to make an appropriate determination of their agroforestry potential in Canada. General predictions of the importance of various ecological considerations for aspen agroforestry systems suitable for north temperate and boreal regions of Canada are provided in the following sections.

Expected Resource Partitioning in Aspen Agroforests

During the herbaceous phase, growth will be strongly influenced by the relative supply and partitioning of both light and soil resources. The ability to intercept light is a function of leaf area and canopy hierarchy. Small differences in canopy size or height should confer large advantages in intercepting light. Similarly, competition for soil water and nutrients should be acute in mixtures of aspen seedlings and herbaceous species with a competitive advantage conferred on the species with larger root volumes or rapidly spreading root profiles (either horizontally or vertically). Therefore, resource partitioning in mixtures of aspen seedlings and herbaceous vegetation should be determined largely by species-specific traits and adaptations.

Size asymmetry during the intermediate and arboreal phases dictates that light availability will be determined by the level of aspen cover. A positive understory production response is predicted for incremental PAR increases between individual species' light compensation and saturation points. Soil-based interactions should also tend towards asymmetric resource use by aspen during these phases with a net increase in understory production with reduced below-ground interactions.

Complementary use of soil resources can occur with physical separation of the overstory and understory rooting profiles, or temporal separation of soil resource use. However, a strong separation of rooting zones is unlikely in aspen agroforestry systems in north temperate or boreal environments. The majority of aspen roots are concentrated in the upper 20 cm of boreal soils, and there is a negative correlation between understory herb cover and aspen root density (Strong and La Roi 1983). Temporal separation of resource use may occur in aspen agroforestry systems, with aspen most likely to begin using soil resources earlier than herbaceous vegetation (Johnston 1970). This may promote complementary use, or it may give aspen a competitive advantage through pre-emptive use of limiting resources.

Above- and Below-ground Interactions?

Depending on the phase of agroforestry development and individual herbaceous species' adaptations, positive or negative interactions between above and below-ground effects may be expected in aspen-forage systems in Canada. Cahill (2002) predicted:

1. positive interactions (combined effects greater than the sum of their individual effects) in environments where species can reach the upper plant canopy; and,
2. negative interactions (combined effects less than the sum of their individual effects) where both root and shoot competition severely limit plant growth (as in a forest understory).

Thus, a positive interaction between above- and below-ground effects may occur during the herbaceous phase, while negative interactions are more likely to occur in intermediate or arboreal phases of agroforestry production.

Net Facilitation or Competition?

In mixtures of tree seedlings and herbaceous vegetation, net competition is generally experienced by the tree seedlings. Evidence for the benefits of vegetation control around tree seedlings is "widespread and long-term" (Nambiar and Sands 1993). This is especially true of planting tree species into established herbaceous vegetation where the herbaceous species have deeper, denser root systems and may compete strongly for water, nutrients and light (Schroth 1999). Most studies however, have not attempted to determine the form of competition (light versus soil resources), or to identify facilitative effects. Aspen seedlings will likely experience competitive growth suppression when grown with herbaceous species. However, the potential for facilitating processes also resultant from an herbaceous ground cover to mitigate competitive effects is not known.

Root-shoot separation studies in other established agroforestry combinations suggest below-ground competition is the predominant interaction influencing understory productivity, with evidence for neutral or net facilitation resulting from partial tree cover. However, this evidence is predominantly from arid, low-latitude ecosystems, and therefore need to be tested at northern latitudes where solar input may have a stronger influence because of both the low solar angle and shorter growing season.

Theory on the balance between facilitation and competition predicts that net facilitation will be expressed in "harsh" environments (Bertness and Callaway 1994, Brooker and Callaghan 1998, Holmgren *et al.* 1997). What constitutes a harsh environment is contextual to the local range of conditions and individual plant species adaptations. The boreal zone has been characterized as harsh for plant growth because of both a short growing season and cold, relatively nutrient poor soils (Bonan and Shugart 1989). Therefore, even relatively brief periods of moisture or T stress may strongly reduce total annual production. Likewise, seemingly minor changes in soil nutrient status, soil T, or the length of the growing period (e.g. through early or late season frost) can have significant impacts on seasonal productivity. Cyclical droughts may also convey a temporal aspect to competition-facilitation dynamics. Facilitation of soil moisture through reduced evaporation in the understory is regularly observed in arid ecosystems. The same facilitation may be expected to have a strong effect on production in more mesic or hygric zones during a drought year, but may be insignificant relative to competitive processes with more abundant precipitation.

New Information Needed

The relative importance of different processes and variables in determining the agroforestry potential of mixing aspen and understory crop production in Canada requires new site and species-specific information. Consideration for the simultaneous occurrence of competitive and facilitative effects, with above- and below-ground processes and temporal variability must be emphasized in agroforestry research. Research is therefore needed in mixtures of aspen and herbaceous species to determine:

1. the predominance and form of competitive and facilitative effects;
2. how these effects vary with environmental gradients;
3. how these interactions vary with the phase of agroforest development; and,
4. how temporal variation in resource availability and environmental conditions influence seasonal productivity.

2.5 Literature Cited

Anderson, R.C., O.L. Loucks and A.M. Swain. 1969. Herbaceous response to canopy cover, light intensity and throughfall precipitation in coniferous forests. Ecology 50: 255-263.

Bailey, A.W., and R.K. Gupta. 1973. Grass – woody plant relationships. Canadian Journal of Plant Science 53: 671-676.

Belsky, A.J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients and tree-grass competition. Ecology 75: 922-932.

Belsky, A.J., R.G. Amundson, J.M. Duxbury, S.J. Riha, A.R. Ali and S.M. Mwonga. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology 26: 1005-1024.

Bergez, J.E., M. Etienne, and P. Balandier. 1999. ALWAYS: a plot-based silvopastoral system model. Ecological Modeling 115: 1-17.

Bertness, M.D. and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9: 191-193.

Blair, R.M. and H.G. Enghardt. 1976. Deer forage and overstory dynamics in a loblolly pine plantation. Journal of Range Management 29: 104-108.

Bonan, G.B., and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecological Systems 20: 1-28.

Brenner, A.J. 1996. Microclimate modifications in agroforestry. Pages 159-187 *in*: Ong, C.K. and P. Huxley (editors). Tree-Crop Interactions: A Physiological Approach. CAB International, Cambridge, UK, 386 p.

Brinkman, K.A. and E.I. Roe. 1975. Quaking aspen: silvics and management in the Lake States. USDA, Forest Service, Agriculture Handbook No. 486, Washington, DC, 52 p.

Brooker, R.W. and T.V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos 81: 196-207.

Brown, H.E. and J.R. Thompson. 1965. Summer water use by aspen, spruce, and grassland in Western Colorado. Journal of Forestry 63: 756-760.

Buck, M.G. 1986. Concepts of resource sharing in agroforestry. Agroforestry Systems 4: 191-203.

Cahill, J.F. Jr. 1999. Fertilization effects on interactions between above- and belowground competition in an old field. Ecology 80: 466-480.

Cahill, J.F. Jr. 2002. Interactions between root and shoot competition vary among species. Oikos 99: 101-112.

Caldwell, M.M., T.E. Dawson and J.E. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia 113: 151-161.

Callaway, R.M. and L.R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958-1965.

Callaway, R.M., N.M. Nadkarni and B.E. Mahall. 1991. Facilitation and interference of *Quercus douglassii* on understory productivity in Central California. Ecology 72: 1484-1499.

Campbell. C.D., D. Atkinson, P.G. Jarvis and P. Newbould. 1994. Effects of nitrogen-fertiliser on tree/pasture competition during the establishment phase of a silvopastoral system. Annals of Applied Biology 124: 83-96.

Cannell, M.G.R. and J. Grace. 1993. Competition for light: detection, measurement and quantification. Canadian Journal of Forest Research 23: 1969-1979.

Carlson, D.H., S.H. Sharrow, W.H. Emmingham and D.P. Lavender. 1994. Plant-soil-water relations in forestry and silvopastoral systems in Oregon. Agroforestry Systems 25: 1-12.

Chapin, F.S. III, A.J. Bloom, C.B. Field and R.H. Waring. 1987. Plant responses to multiple environmental factors. BioScience 37: 49-57.

Clary, W.P. 1969. Increasing sampling precision of some herbage variables through knowledge of the timber overstory. Journal of Range Management 22: 200-201.

Clary, W.P. and D.C. Morrison. 1973. Large alligator junipers benefit early-spring forage. Journal of Range Management 26: 70-71.

Clinton, P.W., C.M. Frampton and D.J. Mead. 1994. Modeling competitive pasture effects on nutrient uptake by *Pinus radiata*. New Zealand Journal of Forestry Science 24: 268-278.

Clinton, P.W. and D.J. Mead. 1993. Competition for nitrogen between *Pinus radiata* and pasture. I. Recovery of ^{15}N after one growing season. Canadian Journal of Forest Research 24: 882-888.

Constabel, A.J. and V.J. Lieffers. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Canadian Journal of Forest Research 26: 1008-1014.

Coomes, D.A. and P.J. Grubb. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs 70(2): 171-207.

Dang, Q-L., H.A. Margolis, M.R. Coyea, M. Sy and G.J. Collatz. 1997. Regulation of branch level gas exchange of boreal trees: roles of shoot water potential and vapour pressure difference. Tree Physiology 17: 521-535.

Daubenmire, R. 1953. Nutrient content of leaf litter of trees in the northern Rocky Mountains. Ecology 34: 786-793.

Davis, M.A., K.J. Wrage and P.B. Reich. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. Journal of Ecology 86: 652-661.

Davis, M.R. 1995. Influence of radiata pine seedlings on chemical properties of some New Zealand montane grassland soils. Plant and Soil 176: 255-262.

Davis, M.R. and M.H. Lang. 1991. Increased nutrient availability in top soils under conifers in the South Island high country. New Zealand Journal of Forestry Science 21: 165-179.

Dawson, L.A., E.I. Duff, C.D. Campbell and D.J. Hirst. 2001. Depth distribution of cherry (*Prunus avium* L.) tree roots as influenced by grass root competition. Plant and Soil 231: 11-19.

DeByle, N.V. 1976. The aspen forest after harvest. *In:* Utilization and marketing tools for aspen management in the Rocky Mountains: Proceedings of the symposium. General Technical Report RM-29, USDA, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, pp 35-40.

Ehrenreich, J.H. and J.S. Crosby. 1960. Herbage production is related to hardwood crown cover. Journal of Forestry 58: 564-565.

Eissenstat, D.M. and J.E. Mitchell. 1983. Effects of seeding grass and clover on growth and water potential of Douglas-fir seedlings. Forest Science 29: 166-179.

Ellis, R.E. 1986. Understory development in aspen-white spruce forests in northern Alberta. Master of Science thesis, University of Alberta, Edmonton, AB, 84 p.

Ellison, L. and W.R. Houston. 1958. Production of herbaceous vegetation in openings and under canopies of western aspen. Ecology 39: 337-345.

Frost, W.E. and N.K. McDougald. 1989. Tree canopy effects on herbaceous production of annual rangeland during drought. Journal of Range Management 42: 281-283.

Ffolliot, P.F. 1983. Overstory-understory relationships in western forests: ponderosa pine forests. Colorado State University Experimental Station, Western Regional Research Publication 1, Denver, CO, pp 13-18.

Genoway, P. 1999. Suckering potential of declining aspen and mixedwood stands in West-Central Saskatchewan. Master of Science Thesis, University of Alberta, Edmonton, AB, 120 p.

Gleeson, S.K. and D. Tilman. 1992. Plant allocation and the multiple limitation hypothesis. The American Naturalist 139: 1322-1343.

Goldberg, D. and A. Novoplansky. 1997. On the relative importance of competition unproductive environments. Journal of Ecology 85: 409-418.

Grelen, H.E. and R.E. Lohrey. 1978. Herbage yields related to basal area and rainfall in a thinned longleaf plantation. Research Note SO-232, USDA, Forest Service, Southern Forest Experimental Station, New Orleans, LA, 4 p.

Grime, J. 1979. Plant Strategies and Vegetation Processes. John Wiley, New York.

Guevara-Escobar, A., W.R.N. Edwards, R.H. Morton, P.D. Kemp and A.D. Mackay. 2000. Tree water use and rainfall partitioning in a mature poplar-pasture system. Tree physiology 20: 97-106.

Gyenge, J.E., M.E. Fernandez, G. Dalla Salda and T.M. Schlichter. 2002. Silvopastoral systems in Northwestern Patagonia II: water balance and water potential in a stand of *Pinus ponderosa* and native grassland. Agroforestry Systems 55: 47-55.

Haines, S.G., L.W. Haines and G. White. 1978. Leguminous plants increase sycamore growth in Northern Alabama. Soil Science Society of America Journal 42: 130-132.

Halls, L.K. and J.L. Schuster. 1965. Tree-herbage relations in pine-hardwood forests of Texas. Journal of Forestry 63: 282-283.

Halls, L.K. and R.F. Suman. 1954. Improved forage under southern pines. Journal of Forestry 52: 848-851.

Harris, N.R. 1998. Spatial patterns of tree effects on pasture production in open canopied agroforests. Master of Science Thesis, Oregon State University, Corvallis, OR, 109 p.

Hogg, E.H., B. Saugier, J-Y. Pontailler, T.A. Black, W. Chen, P.A. Hurdle and A. Wu. 2000. Responses of trembling aspen and hazelnut to vapour pressure deficit in boreal deciduous forest. Tree Physiology 20: 725-734.

Holmgren, M., M. Scheffer and M.A. Huston. 1997. The interplay of facilitation and competition in plant communities. Ecology 78: 1966-1975.

Horn, J.C. 1985. Responses of understory tree seedlings to trenching. American Midland Naturalist 114: 252-258.

Huffman, R.D., M.A. Fajvan and P.B. Wood. 1999. Effects of residual overstory on aspen development in Minnesota. Canadian Journal of Forest Research 29: 284-289.

Joffre, R. and S. Rambal. 1993. How tree cover influences the water balance of Mediterranean rangelands. Ecology 74: 570-582.

Johnson, M.K., L.G. Davis, K.F. Ribbeck, J.H. Render and H.A. Pearson. 1986. Management of subterranean clover in pine forested range. Journal of Range Management 39: 454-456.

Johnston, R.S. 1970. Evapotranspiration from bare, herbaceous and aspen plots: A check on a former study. Water Resources Research 6: 324-327.

Jose, S., A.R. Gillespie, J.R. Seifert and D.F. Biehle. 2000. Defining competition vectors in a temperate alley cropping system in the midwestern USA. Agroforestry Systems 48: 41-59.

Kho, R.M. 2000. A general tree-environment-crop interaction equation for predictive understanding of agroforestry systems. Agriculture, Ecosystems and Environment 80: 87-100.

Kho, R.M., B. Yacouba, M. Yaye, B. Katkove, A. Moussa, A. Iktam and A. Mayaki. 2001. Separating the effects of trees on crops: the case of *Faidherbia albida* and millet in Niger. Agroforestry Systems 52: 219-238.

Landhäusser, S.M., K.J. Stadt and V.J. Lieffers. 1997. Photosynthetic strategies of summergreen and evergreen understory herbs of the boreal mixedwood forest. Oecologia 112: 173-178.

Landsburg, J.J. 1986. Physiological Ecology of Forest Production. Academic Press, Toronto, pp 32-37.

Lewis, S.L. and E.V.J. Tanner. 2000. Effects of above- and belowground competition on growth and survival of rainforest tree seedlings. Ecology 81:2525-2538.

Lieffers, V.J. and K.J. Stadt. 1993. Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Canadian Journal of Forest Research 24: 1193-1198.

Lieffers, V.J., K.J. Stadt, and S. Navratil. 1996. Age structure and growth of understory white spruce under aspen. Canadian Journal of Forest Research 26: 1002-1007.

Man, R. and V.J. Lieffers. 1997. Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open. Tree Physiology 17: 437-444.

Man, R. and V.J. Lieffers. 1999. Are mixtures of aspen and white spruce more productive than single species stands? The Forestry Chronicle 75: 505-513.

Marsden, B.J., V.J. Lieffers and J.J. Zwiazek. 1996. The effect of humidity on photosynthesis and water relations of white spruce seedlings during the early establishment phase. Canadian Journal of Forest Research 26: 1015-1021.

McClaran, M.P. and J.W. Bartolome. 1989. Effect of *Quercus douglasii* (Fagaceae) on herbaceous understory along a rainfall gradient. Madrono 36: 141-153.

McKenzie, D., C.B. Halpern, and C.R. Nelson. 2000. Overstory influences on herb and shrub communities in mature forests of western Washington, U.S.A. Canadian Journal of Forest Research 30: 1655-1666.

McPherson, G.R. and H.A. Wright. 1990. Effects of cattle grazing and *Juniperus pinchotii* canopy cover on herb cover and production in Western Texas. American Midland Naturalist 123: 144-151.

Messier, C. 1996. Managing light and understory vegetation in boreal and temperate broadleaf-conifer forests. pp 59-81 *in*: Comeau, P.G. and K.D. Thomas (editors). Silviculture of temperate and boreal broad leaf-conifer mixtures. Province of British Columbia, Ministry of Forests Research Program, Victoria, BC.

Miller, A.W. and S.G. Pallardy. 2001. Resource competition across the crop-tree interface in a maize-silver maple temperate alley cropping stand in Missouri. Agroforestry Systems 53: 247-259.

Miller, B.J., P.W. Clinton, G.D. Buchan and A.B. Robson. 1998. Transpiration rates and canopy conductance of Pinus radiata growing with different pasture understories in agroforestry systems. Tree Physiology 18: 575-582.

Mitchell, J.E. and P.N.S. Bartling. 1991. Comparison of linear and non-linear overstory-understory models for ponderosa pine. Forest Ecology and Management 42: 195-204.

Monk, C.D. and F.C. Gabrielson. 1985. Effects of shade, litter and root competition on old field vegetation in South Carolina. Bulletin of the Torrey Botanical Club 112: 383-392.

Moore, M.M. and D.A. Deiter. 1992. Stand density index as a predictor of forage production in northern Arizona pine forests. Journal of Range Management 45: 267-271.

Montieth, J.L. 1977. Climate and efficiency of crop production in Britain. Philosophical Transactions of the Royal Society of London B 281: 277-294.

Mueggler, W.F. and D.L. Bartos. 1977. Grindstone Flat and Big Flat exclosures - a 41-year record of changes in clearcut aspen communities. Research Paper INT-195, USDA, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, 16 p.

Nambiar, E.K.S. and R. Sands. 1993. Competition for water and nutrients in forests. Canadian Journal of Forest Research 23: 1955-1968.

Nams, V.O., N.F.G. Folkard, and J.N.M. Smith. 1993. Effects of nitrogen fertilization on several woody and non-woody boreal forest species. Canadian Journal of Botany 71: 93-97.

Nemati, N. and H. Goetz. 1995. Relationships of overstory to understory cover variables in a ponderosa pine/gambel oak ecosystem. Vegetatio 119: 15-21.

Olofsson, J., J. Moen and L. Oksanen. 1999. On the balance between positive and negative interactions in harsh environments. Oikos 86: 539-543.

Ong, C.K. 1996. A framework for quantifying the various effects of tree-crop interactions. Pages 1-23 *in*: Ong, C.K. and P. Huxley (editors). Tree-Crop Interactions: A Physiological Approach. CAB International, Cambridge, UK, 386 p.

Pare, D. and Y. Bergeron. 1996. Effects of colonizing tree species on soil nutrient availability in a clay soil of the boreal mixedwood. Canadian Journal of Forest Research 26: 1022-1031.

Pearson, H.A., M.L. Elliott-Smith, A. Martin Jr., and V.C. Baldwin. 1994. Subterranean clover: Nutrients for pines. Pages 17-20 i*n*: Symposium on Current Research in the Chemical Sciences: Third Annual Southern Station Chemical Sciences Meeting. General Technical Report SO-101, USDA, Forest Service, Southern Forest Experiment Station, New Orleans, LA.

Peek, J.M., J.J. Korol, D. Gay and T. Hershey. 2001. Overstory-understory biomass changes over a 35-year period in south central Oregon. Forest Ecology and Management 150: 267-277.

Penaloza, R., M. Herve and L. Sobarzo. 1985. Applied research on multiple land use through silvopastoral system in Southern Chile. Agroforestry Systems 3: 59-77.

Perala, D.A. and D.H. Alban. 1982. Biomass, nutrient distribution and litterfall in *Populus*, *Pinus* and *Picea* stands on two different soils in Minnesota. Plant and Soil 64: 177-192.

Percival, N.S. and R.L. Knowles. 1988. Relationship between radiata pine and understory pasture production. *In:* Maclaran, P. (editor). Proceedings of the Agroforestry Symposium, Rotorua, 24-27 November 1986, FRI Bulletin No. 139, Ministry of Forestry, Forest Research Institute, Rotorua, New Zealand, pp 152-160.

Pieper, R.D. 1990. Overstory-understory relations in pinyon-juniper woodlands in New Mexico. Journal of Range Management 43: 413-415.

Pugnaire, F.I., P. Haase and J. Puigdefábregas. 1996. Facilitation between higher plant species in a semi-arid environment. Ecology 77: 1420-1426.

Putz, F.E. and C.D. Canham. 1992. Mechanisms of arrested development in shrublands: root and shoot competition between shrubs and tree seedlings. Forest Ecology and Management 49: 267-275.

Ratcliff, R.D., D.A. Duncan and S.E. Westfall. 1991. California oak-woodland overstory species affect herbage understory: Management implications. Journal of Range Management 44: 306-310.

Riegel, G.M., R.F. Miller and W.C. Krueger. 1992. Competition for resources between understory vegetation and overstory *Pinus pondersosa* in northeastern Oregon. Ecological Applications 2: 71-85.

Roden, J.S. and R.W. Pearcy. 1993. Effects of leaf flutter on the light environment of poplars. Oecologia 93: 201-207.

Ross, M.S., L.B. Flanagan, and G.H. La Roi. 1986. Seasonal and successional changes in light quality and quantity in the understory of boreal forest ecosystems. Canadian Journal of Botany 64: 2792-2799.

Rowe, J.S. 1956. Uses of undergrowth plant species in forestry. Ecology 37: 461-473.

Ruark, G.A. 1990. Evidence for the reserve shelterwood system for managing quaking aspen. Northern Journal of Applied Forestry 7: 58-62.

Salisbury, F.B. and C.W. Ross. 1992. Plant Physiology. Fourth Edition, Wadsworth Publishing Co., Belmont, CA, 682 p.

Scholes, R.J. and S.R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecological Systems 28: 517-544.

Schott, M.R. and R.D. Pieper. 1985. Influence of canopy characteristics of one-seed juniper on understory grasses. Journal of Range Management 38: 328-331.

Schroth, G. 1999. A review of belowground interactions in agroforestry, focusing on mechanisms and management options. Agroforestry Systems 43: 5-34.

Scifres, C.J., J.L. Mutz, R.E. Whitson, and D.L. Drawe. 1982. Interrelationships of huisache canopy cover with range forage on the coastal prairie. Journal of Range Management 35: 558-562.

Severson, K.E. 1982. Production and nutritive value of aspen understory, Black Hills. Journal of Range Management 35: 786-789.

Severson, K.E. and J.J. Kranz. 1976. Understory production not predictable from aspen basal area or density. Research Note RM-314, USDA, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 4 p.

Shepperd, W.D., D.L. Bartos and S.A. Mata. 2001. Above- and below-ground effects on aspen clonal regeneration and succession to conifers. Canadian Journal of Forest Research 31: 739-745.

Shepperd, W.D. and F.W. Smith. 1993. The role of near-surface lateral roots in the life cycle of aspen in the central Rocky Mountains. Forest Ecology and Management 61: 157-170.

Smith, D.M. 2000. Water and climatic relationships in agroforestry. Pages 115-130 *in*: Ashton, M.S. and F.M. Montagnini (editors). The Silvicultural Basis of Agroforestry Systems. CRC Press, New York, 278 p.

Sharrow, S.H. 1991. Tree density and pattern as factors in agrosilvopastoral system design. Pages 242-247 *in:* Garrett, G. (editor). Proceedings of the Second Conference on Agroforestry in North America, August 18-21, Springfield, MO, 114 p.

Sharrow, S.H., D.H. Carlson, W.H. Emmingham and D. Lavender. 1996. Productivity of two Douglas-fir/subterranean clover/sheep agroforests compared to pasture and forest monocultures. Agroforestry Systems 34: 305-313.

Ssekabembe, C.K., P.R. Henderlong and M. Larson. 1994. Soil moisture relations at the tree/crop interface in black locust alleys. Agroforestry Systems 25: 135-140.

Steele, K.W. and N.S. Percival. 1984. Nitrogen fertiliser application to pastures under *Pinus radiata*. New Zealand Journal of Agricultural Research 27: 49-55.

Steneker, G.A. 1976. Guide to the silvicultural management of trembling aspen in the prairie provinces. Information Report NOR-X-164, Canadian Forest Service, Northern Forestry Research Centre, Edmonton, AB, 6 p.

Strong, W.L. and G.H. La Roi. 1983. Rooting depths and successional development of selected boreal forest communities. Canadian Journal of Forest Research 13: 577-588.

Sucoff, E. 1982. Water relations of the aspens. Technical Bulletin 338-1982, University of Minnesota, Agricultural Experiment Station, St. Paul, MN, 36 p.

Swan, J.M.A. and R.L. Dix. 1966. The phytosociological structure of upland forest at Candle Lake, Saskatchewan. Journal of Ecology 54: 13-40.

Tapia, L.A.B., P.F. Ffolliott and D.P. Guertin. 1990. Herbage production - forest overstory relationships in two Arizona ponderosa pine forests. Journal of Range Management 43: 25-28.

Tappe, P.A., M.G. Shelton and T.B. Wigley. 1992. Overstory – understory relationships in natural loblolly pine – hardwood stands: implications for wildlife habitat. *In*: Proceedings of the Seventh Biennial Southern Silvicultural Research Conference. General Technical Report SO-93, USDA, Forest Service, Southern Forest Experimental Station, New Orleans, LA, pp 613-619.

Taylor, D.R., L.W. Aarssen and C. Loehle. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat template for plant life history strategies. Oikos 58: 239-250.

Teague, W.R., S.L. Dowhaver, S.G. Whisenant and E. Flores-Anara. 2001. Mesquite and grass interference with establishing redberry juniper seedlings. Journal of Range Management 54: 680-684.

Tew, R.K. 1968. Properties of soil under aspen and herb-shrub cover. Research Note INT-78, USDA, Forest Service, Intermountain Forest and Range Experiment Station, Odgen, UT, 4 p.

Tiedemann, A.R. and J.O. Klemmedson. 1977. Effect of mesquite trees on vegetation and soils in the desert grassland. Journal of Range Management 30: 361-367.

Trowbridge, R. and F.B. Holl. 1992. Early growth of lodgepole pine after establishment of alsike clover-*Rhizobium* nitrogen-fixing symbiosis. Canadian Journal of Forest Research 22: 1089-1093.

Turkington, R., J. Elizabeth, C.J. Krebs, M.R.T. Dale, V.O. Nams, R. Boonstra, S. Boutin, K. Martin, A.R.E. Sinclair and J.N.M. Smith. 1998. The effects of NPK fertilization for nine years on boreal forest vegetation in northwestern Canada. Journal of Vegetation Science 9:333-346.

Walton, P.D. 1983. Production and Management of Cultivated Forages. Reston Publishing Company, Inc., Reston, Virginia. p 240.

Warner, J.H. 1971. Understory characteristics related to site quality for aspen in Utah. Doctor of Philosophy dissertation, University of Utah, Salt Lake City, UT, 77 p.

Weetman, G.F., H.H. Krause, E. Koller and J.M. Veilleux. 1987. Interprovincial forest fertilization trials 5- and 10- year results. The Forestry Chronicle 63: 184-192.

Weitzman, S. and R.R. Bay. 1963. Forest soil freezing and the influence of management practices, northern Minnesota. USDA, Forest Service, Lake States Forest Experimental Station, St. Paul, MN, Research Paper LS-2, 8 p.

Welden, C.W. and W.L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. The Quarterly Review of Biology 61: 23-44.

Wilson, J.B. 1988. Shoot competition and root competition. Journal of Applied Ecology 25: 279-296.

Wilson, J.R. 1990. The eleventh hypothesis: Shade. Agroforestry Today 2: 14-15.

Wojtkowski, P.A. 1998. The Theory and Practice of Agroforestry Design. Science Publishers Inc., Enfield, NH, 282 p.

Wolters, G.L. 1973. Southern pine overstories influence herbage quality. Journal of Range Management 26: 423-426.

Wolters, G.L. 1982. Longleaf and slash pine decreases herbage production and alters herbage composition. Journal of Range Management 35: 761-763.

Woods, R.F., D.R. Betters and E.W. Mogren. 1982. Understory herbage production as a function of Rocky Mountain aspen stand density. Journal of Range Management 35: 380-381.

Young, D.R. and W.K. Smith. 1982. Simulation studies of the influence of understory location on transpiration and photosynthesis of *Arnica cordifolia* on clear days. Ecology 63: 1761-1770.

Young, D.R. and W.K. Smith. 1983. Effect of cloudcover on photosynthesis and transpiration in the subalpine understory species *Arnica latifolia*. Ecology 64: 681-687.

Younger, P.D., R.G. Koch and L.A. Kapustka. 1980. Allelochemical interference by quaking aspen leaf litter on selected herbaceous species. Forest Science 26: 429-434.

Zinke, P.J. 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43: 130-133.

CHAPTER 3

Competition and Facilitation in Mixtures of Aspen Seedlings, Alfalfa and Marsh Reedgrass

3.1 Introduction

Increasing demand for hardwoods is generating interest in the intensive cultivation of aspen (*Populus tremuloides* Michx.) and related poplar species across the Canadian Prairie Provinces (Balatinecz *et al.* 2001, Ward 2001). Aspen seedlings must compete for light and soil resources with surrounding vegetation, and successful establishment of a new plantation requires control of negative plant-to-plant effects. In mixtures of newly planted tree seedlings and herbaceous vegetation, net competition is generally experienced by the tree seedlings. Evidence for the benefits of vegetation control around tree seedlings is "widespread and long-term" (Nambiar and Sands 1993). This is especially true of tree species planted into established field vegetation where the herbaceous species initially have deeper, denser root systems and can compete strongly for water, nutrients and light (Schroth 1999). Immature aspen have previously been shown to be inferior competitors in mixtures with herbaceous species (Bailey and Gupta 1973, Landhäusser and Lieffers 1998).

Interactions among plants can be a complex mixture of competitive and facilitative processes (Callaway and Walker 1997). Thus, not all interactions among tree seedlings and co-dominant herbaceous vegetation need to be negative. In fact, forages can potentially facilitate tree growth either directly or indirectly. For example, legumes can directly facilitate increased soil nitrogen (N), or may function indirectly, such as by displacing a more competitive species. The potential benefits of mixing tree and forage production can be exploited in two ways: to provide low-input erosion control, fertility or vegetation management in conventional forest plantations or by adopting an agroforestry approach. Agroforestry systems utilize the simultaneous production of trees with other crops to optimize the biological and economic returns from these mixtures (Wojtkowski 1998). Successful utilization of both approaches requires an understanding of the form and relative importance of various processes to ensure the design and manipulation of the system enhances facilitation and/or minimizes competition.

This experiment examined the relative competitive abilities of aspen seedlings, alfalfa and marsh reedgrass in a fixed-density replacement study. Many studies have shown an inverse relationship between plant yield and density, in both monocultures and species mixtures (Jolliffe 1988). In fixed-density experiments however, increases in the proportion of one plant species over another has varying results depending on the competitive ability and facilitative effects of the species involved.

Marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) is a common, often dominant, understory boreal and sub-boreal species that can impede the establishment of aspen and other tree species. It is a strong competitor for soil moisture and nutrients, with up to 80% of its root mass concentrated in the upper 10 cm of the soil profile (Rivard *et al.* 1990). Indeed, under controlled conditions, marsh reedgrass suppressed aspen sucker growth directly through root-based competition, and indirectly through the effects of its leaf litter (Landhäusser and Lieffers 1998). Competitive effects of marsh reedgrass may persist until the forest canopy closes enough that shading suppresses its growth.

Alfalfa (*Medicago sativa* L.) is one of the most widely grown forage crops in the world (Walton 1983). Tap-rooted varieties of alfalfa are able to access deep soil profiles and thus, can potentially minimize surface competition for moisture and nutrients. However, alfalfa cultivars have been bred for rapid, vigorous growth and can competitively suppress other vegetation. In grass-legume mixtures, the grass component typically displaces the legume after a few growing seasons. With alfalfa as the legume component however, the opposite is often true; alfalfa has been widely observed to be an aggressive and persistent species in mixtures (Chamblee 1972). As a cover crop alfalfa may therefore suppress marsh reedgrass and provide an indirect benefit to aspen seedling growth if the competitive effects of alfalfa are less intense than those of reedgrass.

Alfalfa can form symbiotic associations with the N-fixing bacteria *Rhizobium meliloti* and under good growing conditions are capable of fixing in excess of 150 kg N

ha^{-1} yr^{-1} (Walton 1983). Nitrogen fixed by these associations becomes available for uptake by other vegetation when alfalfa leaf litter and root nodules break down and release it into the soil. Increased foliar N and tree growth have been documented in plantation mixtures of tree seedlings and legumes (Carlson *et al.* 1994, Pearson *et al.* 1994, Trowbridge and Holl 1992). To date, N transfer from a legume to aspen has not been documented, although a positive carryover effect of soil enriched from a N-fixing shrub has been demonstrated (Bailey and Gupta 1973). Nor has the facilitative effect of N additions been separated from the changes in competition resulting from the presence of a legume. For example, sycamore (*Platanus occidentalis* L.) seedling growth increased when grown with any one of four herbaceous legumes (Haines *et al.* 1978). Unfortunately however, the experimental design used could not separate the effects of reduced competition resulting from the legumes replacing other vegetation (a weed-suppression effect) from a possible N transfer.

Competition for light and soil resources between aspen seedlings and herbaceous species is expected, and may be intense. However, the overall importance of competitive interactions to aspen growth and survival is not known and must be balanced against other factors. Competition from alfalfa may be greater than any potential benefits of mixing the species, or conversely, N enrichment or other facilitative effects by the alfalfa may offset some or all of its competitive interference. By understanding the balance between these processes, vegetation and fertility management strategies can be developed for aspen plantations that minimize the risk of wind and water erosion associated with removing all co-dominant vegetation to control competition. Likewise, understanding the mix of competitive and facilitative effects can be used to schedule the planting and harvesting of herbaceous crops in agroforestry systems that will retain growth-enhancing processes and mitigate competition with the tree crop.

3.2 Objectives and Hypotheses Tested

The general objective of this experiment was to isolate and quantify the competitive and facilitative processes in mixtures of aspen seedlings, alfalfa and marsh reedgrass. The specific objectives were to determine the effects of varying the proportion of the species at a fixed density on growth and survival of the other species. The null hypotheses tested are listed as follows. Varying the proportion of aspen, marsh reedgrass and alfalfa in fixed-density mixtures has no effect on:

1. aspen damage, survival, height and diameter growth, or mass;
2. marsh reedgrass survival, tiller number or mass;
3. alfalfa survival, root nodulation or mass; and,
4. available soil nitrogen, soil moisture or the proportion of photosynthetically active radiation intercepted.

3.3 Methods

Research Site

This research was conducted on field plots at the University of Alberta's Ellerslie Research Station in Edmonton, Alberta (53° 25' N, 113° 33' W). Ellerslie Research Station is situated in the Aspen Parkland ecoregion (Strong and Leggat 1992) and has a continental climate characterized by cold winters and short, warm summers (1970-2000 average January and July temperatures are -14 and 16°C, respectively). Ellerslie receives an average of 460 mm of precipitation annually with approximately 70% occurring during the May to September growing season. Plots were situated on a deep, silt-clay-loam, Orthic Black Chernozemic soil that has been cultivated with a variety of crops for approximately 50 years.

Treatments and Experimental Design

Aspen, alfalfa and marsh reedgrass were established in 1-m^2 plots at a density of five plants per plot. Plants were arranged with a single plant centered in the middle of the plot and the other four plants equidistantly spaced in a cross-pattern with a 20-cm diagonal spacing from the centre plant (Figure 3-1). The plant species in the focal (centre) position and those in surrounding positions were varied, such that nine plant species combinations were tested: monocultures of each species and 4:1 mixes of two species at a time, in all possible combinations with the single species in the focal position. This design allowed for assessment of the relative competitive and facilitative effects of each species independent of density and spatial effects. Treatments were replicated 10 times each and randomly assigned to plot locations. Plots were weeded by hand throughout the experiment as needed to maintain only the prescribed vegetation in each plot. A 5-m perimeter was established to minimize the risk of agri-chemical drift from adjacent cropping activities. The perimeter was mowed occasionally to minimize edge-effects for the experimental plots.

Alfalfa (cv 'Nordica') was established from seed inoculated with a coating of *Rhizobium meliloti* bacteria in May 2000. Additional plants were established at the same time outside of the experimental plot area to provide alfalfa plants of the same age as those in the experimental units for fill-planting. Because of sporadic germination and mortality due to both wind-driven soil particles and insect defoliation, approximately 95% of the alfalfa planting failed during the first year. Replacements were transplanted on four occasions during the establishment year, of which the latter two transplantations were to replace previous transplants that did not survive. During each transplantation, 100 ml of water was applied to all alfalfa plants (i.e. both newly transplanted and already established plants). A small number of plants were transplanted to replace over-winter mortality in May 2001, coinciding with the planting of the aspen seedlings.

Marsh reedgrass was established from rhizomes in June 2000. Rhizomes were collected the previous day from the Blackfoot Provincial Grazing Reserve (53° 30' N, 113° 03' W), south of Elk Island National Park, Alberta in a Aspen Parkland - Boreal ecoregion transition zone. Rhizomes were cut into 5-cm segments, with each segment containing a live tiller node. Rhizome segments were planted 2-cm deep with the tiller node oriented towards the surface, and each was watered with 100 ml at the time of planting. Approximately 50% of rhizomes sprouted and established marsh reedgrass plants by the end of the first growing season. Surviving plants were excavated in May 2001 at the time of aspen planting and divided into equal-sized plants of 10 to 12 tillers each, which were subsequently replanted to fill the prescribed marsh reedgrass locations.

Aspen seedlings from a common seed lot (1+0 bare root stock) were planted in May 2001. Aspen that died during the first 2 weeks after planting were replaced, after which no plant replacement was conducted. All plots were irrigated over a three week period in May and early June 2001 to counter the effects of low precipitation during the establishment of the aspen seedlings and newly transplanted alfalfa and marsh reedgrass plants. In total, the equivalent of 65.4 mm of precipitation was applied, or approximately equal to the 30-year normal for this period. Aspen seedlings, alfalfa and marsh reedgrass were grown together for 2 growing seasons (May 2001 to July 2002).

Measures

Direct measures of photosynthetically active radiation (PAR, radiation in the 400 to 700 nm bands) were made at the approximate peak standing crop of the perimeter herbaceous species. In 2001, measures were taken in early August with a Decagon AccuPAR™ ceptometer; in 2002, a LICOR, LI-190SA™ quantum sensor was used just prior to the termination of the experiment in mid-July. In each year, PAR sampling was conducted under clear sky conditions, over a 1- to 2-hr period around solar noon. The relative amount of PAR reaching the mid-point of the focal plants in each sampling period was calculated by comparing measures taken within a few seconds of each other at the mid-height of the focal plant and above each plot with an unobstructed sky view. Volumetric soil moisture in the upper 15-cm soil layer of each plot was recorded in 2002 at 3-week intervals with a Delta-T™ theta probe beginning on May 28. Soil moisture readings within each sampling period were taken in the same randomly pre-determined direction from the focal plant, approximately 10-cm from the plot centre. Daily precipitation and air temperatures were recorded with a Campbell Scientific CR10™ weather station located 0.5 km from the research plots.

Monthly assessments of aspen damage and survival of all plants were conducted during the growing seasons of 2001 and 2002. Aspen damage was assessed visually and the proportion of each seedling damaged was estimated on a scale from 1 to 6, corresponding to the classes developed for assessing plant canopy coverage (Daubenmire 1959). Plants were designated as "dead" when no green leaf or stem material was visible.

Baseline measures of aspen height (to the nearest 0.5 cm), root collar diameter (to the nearest 1 mm) and the number of leaf buds were recorded at the time of planting. Aspen height and diameter were measured again at the end of the first growing season (after aspen leaf-fall), the following spring (after the initiation of new leaf growth) and at the termination of the experiment in July 2002. Relative height growth (RGR_H) and relative diameter growth (RGR_D) were determined for each year by dividing the change in each measure from beginning to end of each year, by the measure at the beginning of the year. The number of fully-formed aspen leaves on each seedling was recorded prior to leaf-fall in 2001 and also at the termination of the experiment in 2002. Leaf area was estimated in 2002 for trees in the focal position on a randomly selected subset of 50 leaves from each aspen seedling by direct measurement on a LI-COR, LI-3100™ area meter. Area per leaf (APL) was estimated by dividing the total leaf area by the number of leaves used in the leaf area measurement. Leaf area per tree was estimated by multiplying APL by the number of leaves per tree. Mass of the above-ground portions of the aspen seedlings was determined at the termination of the experiment. Aspen stems were cut from their roots at the root crown. For focal trees, leaves were separated from the stem and weighed separately. For perimeter trees, leaves and stem material (the "shoot") were weighed together. All yield components were dried at 70°C to constant mass, and weighed to the nearest 0.01 g.

The number of marsh reedgrass tillers was recorded at the time of aspen planting, at the end of the 2001 growing season, and again at the termination of the experiment. Above-ground net primary production (ANPP) of alfalfa and marsh reedgrass were estimated by clipping plant material off at ground level in September 2001 and at the termination of the experiment in July 2002. Samples were dried at 70°C to constant mass, and weighed to the nearest 0.01 g. Relative yield total (RYT) for each plant mixture was calculated from the sum of the relative yields (yield per plant in mixture divided by yield per plant in monoculture) of each species.

At the termination of the experiment, five 15-cm deep soil cores were extracted from each plot. At the plot centre, a single 7.6-cm diameter core was collected (the "focal" samples), and four, 3.8-cm diameter cores were collected at the mid-point between the focal plant and each perimeter plant (or planting location for the marsh reedgrass plots) and combined (the "interspace" samples). The volumes of the focal and interspace samples were equivalent (684 cm^3). Soil samples were separated from the air-dried soil cores by screening the contents through a 2-mm Canadian Standard Sieve. Available NO_3-N and NH_4-N were determined by spectral absorption after extraction from the soil with a 5:1 mixture with 2 *M* KCl (Maynard and Kalre 1993).

Roots were separated from the soil cores in a three-phase process. First, the remaining fine soil particles were washed from the root cores with low-pressure through a 1.70-mm Canadian Standard Sieve. The sieve contents were then floated in a container of clean water and extraneous material discarded. The remaining material was strained from the water through a piece of fabric, with recovery of root segments by hand. No attempt was made to separate root content by species and all roots recovered for a given sample were dried at 70°C to constant mass, and weighed to the nearest 0.01 g. Root mass concentrations were calculated by dividing the root mass in each soil core by the soil core volume.

Intensity of competition was calculated for aspen height and diameter growth, RGR_H, RGR_D, leaf number, leaf area, APL, and the mass of all plants as the difference in growth in monoculture from that when grown in combination with the herbaceous species (Appendix 1, Welden and Slauson 1986). The importance of competition to aspen growth relative to differences due to damage was calculated from the ratio of competition intensity to the difference between undamaged and damaged trees for each aspen measure (Welden and Slauson 1986). For the purposes of both these calculations, "optimal" growth was defined as the growth of the aspen in monoculture for any given parameter.

Analyses

Differences in plant mortality and aspen damage were tested with chi-square analyses of the counts between treatment groupings. Damage patterns in the aspen were compared to the size of the aspen using a Kruskal-Wallis test of the rank-sums. Analyses of end measures of aspen mass, leaf area, APL, root mass concentration, and soil nutrients (Tables A2-1 and A2-2, Appendix 2) were conducted with mixed linear models for a completely random design (Littell *et al.* 2002). Annual measures of aspen growth, ANPP of the herbaceous species, indices of competition based on these measures and PAR, as well as monthly measures of soil moisture in 2002 were analyzed with mixed linear models for repeated measures with a completely random design (Table A2-3 and A2-4, Appendix 2). A compound symmetry covariance model was used in the repeated measures analyses. This model was selected iteratively for each response variable by testing several structures and comparing Schwarz's Bayesian information criterion. This criterion test is based on the maximum likelihood fit corrected for the number of parameters in the model, analogous to the adjusted R^2 employed in multiple regression analyses. Species composition of the plots was assumed to have fixed effects and the variation between plots (assessed with replication) was assumed to introduce random effects. A Kenward-Roger correction was applied to the degrees of freedom to eliminate sample size bias. Data were checked for normality and equality of variances and most were found to meet these criteria for parametric analyses. Square-roots were taken of the root mass concentrations, and the NO_3-N data were transformed with a natural logarithm to obtain a normal distribution of the residual errors. Differences among specific treatment effects were separated with individual degree of freedom contrasts.

Growth measures of aspen in the focal plant position were regressed against surrounding biomass, PAR, soil moisture and available N. Likewise, soil moisture and available soil N were regressed against root mass concentrations in each plot. Regressions of multiple independent variables were conducted using both forward stepwise and backward elimination techniques to find the combination and order of variables that produced the best-fit models. Plots of the residual values from the regression equations against their expected values indicated linear models were appropriate for the analyses.

3.4 Results and Discussion

Weather Patterns

The research site experienced two dry growing seasons over the course of the experiment. April to September (inclusive) precipitation in 2000, 2001 and 2002 was 95, 71 and 64%, respectively, of the 30-year normal for this period (Figure 3-2). Total annual precipitation was approximately 433, 266 and 215 mm in 2000, 2001 and 2002 respectively. Conditions were particularly dry during the early part of the growing season in 2002 with only 37% of the normal amount of precipitation during this period. Moreover, precipitation distribution patterns diverged from normal in 2000 and 2001. Early growing season precipitation was generally lower than normal, followed by above-average rainfall in July, creating early season droughts in each of those years. Mean monthly temperatures were generally within the expected range for these periods, with the exception of June and July 2002, when temperatures exceeded the long-term normal by 20 and 27%, respectively.

Photosynthetically Active Radiation

The proportion of open sky PAR reaching the focal plant differed ($p<0.0001$) with perimeter species, reflecting the variable amount of above-ground canopy of each species. The proportion in 2001 was 93 ± 8, 78 ± 9, 38 ± 8% with aspen, marsh reedrass and alfalfa, respectively. PAR interception was also greater ($p<0.0001$) for all species in 2002 than 2001, corresponding to larger plants in 2002. Aspen, marsh reedrass and alfalfa allowed 60 ± 9, 44 ± 9, 17 ± 8% respectively, of open sky PAR to penetrate to the plot middle in 2002. Alfalfa intercepted the greatest amount of PAR in both years. Aspen interception of PAR did not differ ($p=0.12$) from marsh reedgrass, although there was a trend towards greater PAR interception by marsh reedgrass in each year. Independent of perimeter species identity, above-ground mass of surrounding plants accounted for a small, but significant ($R^2=0.26$, $p<0.001$) proportion of PAR variation in both years. Greater PAR interception by alfalfa likely resulted from differences in leaf orientation and area. A high proportion of marsh reedgrass leaves were oriented vertically, allowing for greater light penetration, whereas alfalfa leaves displayed a more random leaf orientation, with greater foliar cover. Although aspen leaves were primarily oriented horizontally, they had a lower foliar density than alfalfa due to greater vertical distribution, resulting in less light interception.

Soil Moisture and Nutrients

Soil moisture levels were highly dynamic in 2002 and varied with the time of sampling ($p<0.0001$), reflecting both previous soil moisture levels and the precipitation pattern, the focal plant species ($p<0.001$) and surrounding plant species ($p=0.02$) (Figure 3-3). While only from a single growing season, the significant interaction ($p<0.001$) of these three variables on soil moisture patterns provide insight into the shifting patterns of competition and facilitation from the presence of herbaceous ground cover. Only 21 mm of precipitation fell in the month preceding the first soil moisture measures in May 2002. Soil moisture content at this time was greatest among monocultures of aspen, and lowest with the presence of marsh reedgrass in any plant position (Figure 3-3). Dry conditions continued, with only 4 mm of precipitation falling up to the next sampling date (10 June). Although absolute soil moisture levels declined, the previous treatment differences remained. Soil moisture levels during the first two months likely resulted from prolonged uptake and use, with the greatest depletion resulting from the diffuse and fibrous root network of marsh reedgrass. A larger amount (28 mm) of rain fell before the next sample date on 2 July, with most received in a single 24-mm event, three days before sampling. As a result, all soil moisture levels increased, with significantly higher levels ($p<0.0001$) associated with the presence of alfalfa, but no difference ($p=0.44$) between aspen, marsh reedgrass or combinations of the two. The higher soil moisture levels with alfalfa cover may have resulted from reduced evaporation from the soil under its well-developed canopy. Less than 2-mm of precipitation fell in the ensuing 2 weeks, and maximum temperatures exceeded 27°C on most days. As a consequence, soil moisture levels declined on all plots resulting in no differences ($p>0.10$) between species combinations.

Available soil N (NO_3-N and NH_4-N) varied with species mixture and position in the plot relative to the focal plant. The differences expressed may have resulted from a combination of N-fixed and released by alfalfa or different rates of root turn-over and differential uptake by the three species. Available NO_3-N was influenced by the species present in both focal ($p<0.0001$) and perimeter ($p<0.0001$) plant positions (Figure 3-4). With the presence of marsh reedgrass in either the focal or perimeter positions, NO_3-N levels did not differ ($p>0.10$) and were consistently lower ($p<0.01$) than combinations of the other two species. As might be expected, average levels of NO_3-N were greatest with alfalfa in the focal position. Nitrate-N levels were also higher ($p=0.06$) in the plant interspace than the focal position of the aspen monoculture, but did not differ ($p>0.10$) with plot location in any combination of aspen and alfalfa. The high NO_3-N levels in the aspen monoculture in the plant interspace corresponded to the lowest root mass concentration among all treatments (Figure 3-5). This indicates aspen monocultures may have had less ability to remove available N. However, NO_3-N levels correlated very weakly ($R^2=0.03$, $p=0.03$) to root mass concentrations, suggesting root absorption properties of the different species may also have factored in N use.

Soil NH_4-N patterns differed from NO_3-N (Figure 3-4). Overall, the range of available NH_4-N was high (22-36 ppm) for this soil type and time of year, and may have been elevated by premature stoppage of root growth and subsequent decomposition resulting from the 2002 drought. Ammonium levels were greatest at the focal position with marsh reedgrass and alfalfa monocultures ($p=0.04$), but overall, levels did not vary with focal ($p=0.16$) or perimeter ($p=0.08$) plant species. However, there were strong NH_4-N differences ($p<0.0001$) relative to the presence of alfalfa in the focal position, an effect not observed ($p>0.10$) with other species. Ammonium levels were lower in the interspace plot positions in comparison to the focal position with alfalfa as the focal species. Moreover, these levels were lower than the amount of NH_4-N in the plant interspace with either marsh reedgrass ($p<0.01$) or aspen ($p=0.02$) as the focal plant. No definitive explanation was found for the positional difference in NH_4-N levels with alfalfa as the focal species, and this phenomenon requires additional investigation. It may have developed from differences in root decomposition resulting from the different root morphologies among the three species. Alfalfa plants examined had a high proportion of large, suberized roots, which may have resisted decay brought on by drought more readily than the smaller roots of aspen and marsh reedgrass. However, similar to NO_3-N patterns, NH_4-N levels only correlated weakly ($R^2=0.10$, $p<0.0001$) to root mass concentrations. Moreover, differences in root morphology do not explain the elevated soil NH_4-N levels in the focal position of these plots where a larger concentration of alfalfa roots was present. Indeed, there was a positive correlation

($R^2=0.36$, $p<0.0001$) between NH_4-N and root mass concentration when alfalfa was in the focal position.

Damage and Survival

Ellerslie proved to be a challenging site for aspen establishment. Three dry growing seasons were compounded by desiccating winds that occasionally rained debris on the site. Coupled with damage from insect pests and deer browsing, 54% of aspen had >5% of their leaf area damaged in the first year. Aspen seedlings were treated with a chemical browsing deterrent (Deer-Away™) at the time of planting and one month later after the trees had fully-formed leaves. This successfully prevented damage until a very large rainfall (60 mm over 48 hours) apparently reduced the effectiveness of the chemical treatment, after which 39% of aspen were browsed over the ensuing week. Following this damage, all research plots were enclosed with a 2-m tall, paige-wire fence, after which no additional browsing occurred.

Aspen grown in monoculture were subject to greater ($p<0.01$, $n=137$) damage than when grown in plant mixtures, due to greater rates of both insect feeding ($p<0.001$) and deer browsing ($p<0.001$) (Figure 3-6). Moreover, damage to aspen seedlings surrounding focal herbaceous species was intermediate to the damage of aspen monocultures and a single aspen surrounded by herbaceous species. Desiccation of the tip of the aspen stem was the only other significant damage to aspen in the first growing season and did not differ ($p=0.65$) between treatments. Three mechanisms may have contributed to the lower damage rates of aspen when grown with herbaceous species. First, herbaceous vegetation may have provided physical protection by dissipating wind, thereby trapping wind-borne material before it reached the trees and preventing desiccation of the growing points. Secondly, herbaceous species may have disrupted the ability of herbivores to find the aspen, creating a "plant defense guild" (Atsatt and O'Dowd 1976). This could have functioned on several levels: by physically disrupting movement of insects from aspen to aspen, by chemically masking the odour of aspen used by insect specialists to locate the trees, or by hiding the aspen from visual detection. Finally, herbs may have provided a more palatable or preferable food alternative to the aspen seedlings in side-by-side choices, thus diverting feeding damage and indirectly providing protection for the trees.

Alternatively, aspen damage patterns evident in the first year may be confounded by differences in tree seedling size between treatments. Aspen grown in monoculture had superior growth rates and it is possible that larger trees may have been more susceptible than smaller trees to damage. Using both diameter and height as the metric for aspen size, a rank-sum analysis indicated larger trees were indeed more likely to be damaged ($p<0.01$). However, because diameter and height were only recorded at the beginning and end of the growing season, and most of the damage occurred during the middle of the growing period, it is unclear if size differences had been expressed at the time of the damage.

Very little damage occurred during the over-winter period following the first growing season (6% of aspen), and despite ubiquitous, small-scale insect feeding damage in the second growing season, only 17% of the tree seedlings had substantial damage (>5% of leaf area) in that period. Furthermore, aspen damage did not differ with plant mixtures in either the over-winter period between 2001 and 2002 ($p=0.44$, $n=136$), or in the 2002 growing season ($p=0.47$, $n=134$).

Despite less than ideal growing conditions and substantial aspen damage, survival of both aspen and the herbaceous species was high (93%) and unaffected ($p=0.33$) by the treatment combinations. After the final establishment transplantations in early June 2001, survival of all species did not differ ($p>0.05$) between treatments in any time period thereafter, up to and including the termination of the experiment.

Aspen Growth

Most aspects of aspen seedling growth were reduced by the presence of either alfalfa or marsh reedgrass. After two growing seasons, aspen cumulatively had an average 28% smaller diameter ($p<0.0001$), 29% less height ($p=0.02$) and 65% less shoot mass ($p<0.01$) when grown with either alfalfa or marsh reedgrass compared to those grown with conspecifics. In both years, focal aspens had less diameter growth ($p<0.01$) and lower RGR_D ($p<0.001$) when mixed with the herbaceous species compared to monocultures of trees (Table 3-1). Similarly, focal aspen with herbaceous competitors had less total leaf area ($p<0.001$) and APL ($p<0.001$), as well as lower stem ($p=0.01$), leaf ($p<0.01$) and total shoot mass ($p<0.01$) at the end of the experiment than those grown in monoculture.

Alfalfa and marsh reedgrass generally did not differ in their effects on aspen growth. Aspen diameter growth ($p=0.98$), RGR_D ($p=0.53$), leaf area ($p=0.16$) and leaf mass ($p=0.56$), stem mass ($p=0.51$) and shoot mass ($p=0.52$) were all similar with the presence of either herbaceous species (Table 3-1). Conversely, APL was different ($p<0.001$) between all treatments, with marsh reedgrass the most detrimental to aspen leaf size. Likewise, herbaceous species affected some aspects of aspen growth differently in each growing season. For example, although the height of aspen was lower ($p=0.03$) when grown with alfalfa in 2001, growth in monoculture did not differ ($p=0.72$) from those grown with marsh reedgrass (Table 3-1). In 2002, however, aspen had less ($p<0.001$) height growth when grown with either herbaceous species. Similarly, aspen leaf numbers were not affected by plant species in the first growing season ($p=0.80$) but were correlated ($p<0.01$) to the initial number of leaf buds on each aspen seedling. In contrast, aspen with either herbaceous competitor had fewer leaves ($p<0.001$) in 2002. Aspen RGR_H was unaffected ($p=0.88$) by species in either year.

The similarity of effects from alfalfa and marsh reedgrass on aspen was also evident in the intensity of competition expressed on focal aspen seedlings. Interspecific competition on aspen diameter growth ($p<0.01$), leaf number ($p=0.03$), leaf mass ($p<0.01$), stem mass ($p=0.01$), shoot mass ($p=0.02$), leaf area ($p<0.0001$) and APL ($p<0.0001$) were all more intense than with aspen in monoculture (Table 3-2). Intensity of competition from alfalfa and marsh reedgrass differed only in their effects on aspen height growth in 2001 ($p=0.03$) and APL ($p<0.001$) at experiment end. In fact, aspen height growth was limited more by intraspecific competition during the first growing ($p=0.03$) than when combined with marsh reedgrass, as evidenced by a negative intensity of competition value for marsh reedgrass effects on height growth (Table 3-2).

The importance of competition relative to the effects of damage on aspen growth was also calculated to compare the competition results in the context of the broader range of factors affecting aspen growth. Paradoxically, damaged aspen grew better than undamaged aspen in both years of the study (see negative importance of competition values, Table 3-2). Herbaceous species did influence the relative importance of competition, but obviously, the overall importance of damage in this experiment was inconsequential to aspen growth given its outcome. Once again, the average size of trees that were damaged may have confounded these data. That is, trees that had already grown substantially in a given year may have been more susceptible to damage, thus giving the appearance that damaged trees grew better than undamaged trees.

Importance of competition is the ratio of the deviation in growth from optimum due to competitive effects, to the deviation from optimum due to other factors (in this case, damage). Ratios greater than 1 indicate greater importance of competition, while ratios less than 1 indicate greater importance of damage. Using these criteria, diameter and height growth ratios in the first year indicate damage had a greater influence on aspen than competition, albeit from generating a positive effect (Table 3-2). For diameter and height growth in 2002 and in all other aspects of aspen growth, competition was more important than damage. Alfalfa and marsh reedgrass only differed in their influence on the importance of competition for height growth in 2001 (alfalfa more detrimental, $p=0.06$) and APL (marsh reedgrass more detrimental, $p<0.001$).

Aspen growth and end measures were correlated to the mass of surrounding plants and several environmental variables. Across both years of the study, PAR correlated to aspen RGR_D ($R^2=0.17$, $p<0.01$) and was weakly associated with RGR_H ($R^2=0.09$, $p=0.06$). Aspen measures in 2002 could be correlated to a broader range of variables due to the destructive vegetation sampling conducted in that year. Soil moisture and available soil N were found to be important factors relating to most aspects of aspen growth (Table 3-3). Soil moisture levels from June to mid-July and PAR explained 58% of the variability in RGR_D ($p<0.0001$), but none of the variables in 2002 related to RGR_H ($p=0.18$). Aspen leaf number in 2002 was positively correlated ($R^2=0.43$, $p<0.01$) to a combination of early and mid season soil moisture levels, available NH_4-N, and the mass of surrounding vegetation, whereas leaf area was best explained ($R^2=0.62$,

$p<0.0001$) by late May and mid-July soil moisture and the mass of surrounding vegetation. Aspen shoot mass correlated well ($R^2=0.53$, $p<0.001$) with soil moisture levels during the drought period, available N and the mass of surrounding vegetation. Where significant, aspen characteristics were always negatively correlated to the mass of surrounding vegetation and the level of NH_4-N, and positively correlated to most of the soil moisture levels (see regression coefficients, Table 3-2). The one exception was a negative correlation of RGR_D to the 2 July soil moisture levels. Soil moisture at that time showed a positive relationship to plant cover after a large pulse of precipitation, followed by dry conditions. Thus, the negative correlation may have resulted from colinearity of these soil moisture levels with the season-long competitive effects of surrounding plant cover.

Herbaceous Species Growth and Relative Yields

Total ANPP of herbaceous species in monoculture varied ($p=0.02$) with growing season. Alfalfa developed more rapidly and outyielded ($p<0.0001$) marsh reedgrass in both 2001 and 2002, this despite the fact that alfalfa yields decreased from 2001 to 2002 ($p=0.05$) while ANPP of marsh reedgrass in monoculture more than doubled in the same period ($p=0.05$). Moreover, in comparing yields from monocultures and mixtures of aspen and marsh reedgrass, total ANPP decreased with increasing proportion of marsh reedgrass in 2001. One year later, production from the species mixes were similar ($p=0.23$) independent of species ratios, due to increased production of marsh reedgrass. Similarly, focal plant mass differed between the two herbaceous species ($p<0.0001$) in both 2001 and 2002, but overall were unaffected ($p=0.27$) by surrounding species (Table 3-4). However, marsh reedgrass tillering was affected by mixture with other species. Tillering increased each year ($p<0.0001$) and was significantly greater ($p<0.0001$) when grown alone than when either aspen or alfalfa were present as the companion species in 2001. In 2002, marsh reedgrass tiller numbers were again reduced by both aspen and alfalfa, with the latter causing the greatest decrease (Table 3-5). Tiller mass however, did not differ with competitors ($p=0.60$) in either year.

Using above-ground biomass as the measure of plant performance, relative yield totals (RYT) give further insight into the net effects of competition, facilitation and niche separation in these species mixtures (Vandermeer 1989). The RYT reflect the combined production of biomass, and in this experiment, species mixtures resulted in either neutral effects (i.e. equal to monoculture yields) or underyielding. Overyielding, or greater total production from mixtures compared to the combined equivalent area in monoculture, was not observed. With aspen in the focal position, RYT did not differ ($p=0.20$) with either alfalfa or marsh reedgrass competitors, although there was a trend towards declining RYT in the mixture with marsh reedgrass (Table 3-6). Likewise, with alfalfa in the focal position, RYT were not significantly different from monoculture yields. Mixtures with marsh reedgrass in the focal position however, significantly ($p=0.05$) underyielded. Specifically, aspen seedlings in the perimeter positions generated the lowest RYT, likely as a consequence of the reedgrass suppressing the surrounding tree seedling growth.

Root Mass Concentration and Alfalfa Nodulation

Differences in root distributions were evident in the concentration of roots in the upper 15-cm of soil (Figure 3-5). The large taproot of alfalfa accounted for a much greater root mass in the focal position than either marsh reedgrass ($p<0.0001$) or aspen ($p<0.0001$). All three species in monoculture displayed greater ($p<0.0001$) roots in the focal position in comparison to the plot interspace positions. There was a large separation however, in the magnitude of this difference. Aspen and alfalfa had focal root mass concentrations 58 and 50 times greater, respectively, than in the interspace positions, whereas, marsh reedgrass had only 5 times more root mass in the focal position due to a more diffuse root distribution throughout the plots. Indeed, in the plant interspace, the concentration of roots was always greatest with the presence of marsh reedgrass. This large surface root mass may have accounted for the lower levels of soil moisture and NO_3-N associated with marsh reedgrass in plant mixtures. Although overall there were weak or no relationships between root mass concentration and soil moisture and nutrients, there were substantially better correlations between these variables when plots with marsh reedgrass in the competitor position were looked at in isolation. With marsh reedgrass as the perimeter species, root mass concentration was correlated to NO_3-N ($R^2=0.43$, $p<0.0001$), NH_4-N ($R^2=0.10$, $p=0.02$), 28 May soil moisture ($R^2=0.41$, $p<0.001$), 10 June soil moisture ($R^2=0.15$, $p=0.04$), 2 June soil moisture ($R^2=0.18$, $p=0.02$), and 15 July soil moisture ($R^2=0.20$, $p=0.02$).

Alfalfa plants excavated in 2001 from an area adjacent to the research site (planted at the same time as the experimental units to supply replacement plants) had a sparse assortment of 0.5- to 1-cm diameter root nodules. In 2002, the tap root section of each alfalfa plant was excavated and inspected after ANPP and soil core samples were collected. No nodulation was recorded from either the root cores or from plants dug up for inspection at the termination of the experiment in 2002. The severe drought conditions in 2002 most likely impaired nodulation, and may have hastened root turn-over rates in the final year of the study.

Summary and Conclusions

Competition and facilitation were evident in the early dynamics of aspen-forage mixtures with net competition expressed in most aspects of tree seedling growth. Both alfalfa and marsh reedgrass depleted soil moisture faster than pure aspen stands during extended periods of uniform precipitation. Moreover, alfalfa reduced the amount of PAR reaching aspen seedlings. These effects combined to reduce aspen growth but did not increase aspen mortality. Conversely, alfalfa conserved soil moisture in the short-term after substantial rainfall. This may have significant implications for aspen plantations in situations where the majority of growing season precipitation is pulsed in relatively brief periods, interspersed with prolonged drought. Nevertheless, it is important to emphasize that under the conditions of this experiment, aspen RGR_D was negatively correlated to the elevated soil moisture under alfalfa after a large rainfall pulse. This is likely because the soil moisture effects were coupled with significant PAR interception also resultant from the legume canopy, and heavy rainfall interspersed with drought occurred only once, rather than as the predominant precipitation pattern. Soil moisture conservation, may therefore be less important to aspen growth relative to PAR interception until the trees elevate their canopy above the herbaceous ground cover.

Aspen grown in plant mixtures had less damage during the first growing season, which may have been due to protection by the herbaceous species, although as previously noted, this is potentially confounded by tree size. In addition, soil NO_3-N was elevated under alfalfa, with similar levels where alfalfa was planted with aspen. In comparison, alfalfa combined with marsh reedgrass, displayed levels of NO_3-N as low as the marsh reedgrass monoculture, indicating any net N evolution from the alfalfa was likely negated by absorption by the marsh reedgrass. The increase in soil N from alfalfa after three growing seasons has positive implications for aspen plantation management and developed earlier than results from other forest plantations have indicated. For example, Trowbridge and Holl (1992) found both increased needle mass and foliar N concentrations in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) grown with alsike clover (*Trifolium hybridum* L.) than those grown without, but only after four years. Similarly, pines absorbed and translocated N fixed by subterranean clover only after several years of soil N accumulation (Pearson *et* al. 1994).

Some aspects of facilitation displayed a strong temporal nature, as in the short-term moisture conservation from alfalfa, and the sheltering effects by herbaceous species in reducing early damage to tree seedlings. Thus, facilitation may be important in eliminating negative threshold events in early plantation dynamics (e.g. to slow soil moisture loss after infrequent rainfall, or by reducing the extent of a particularly acute damage event), but is otherwise absent or masked by more persistent competitive effects.

From an agroforestry perspective, using alfalfa as a short-term cover crop for vegetation or fertility management therefore may have some merit. By this management scheme, alfalfa could be established prior to, or concurrently with, aspen planting, and removed from the stand with tillage or herbicides in the first year after outplanting trees. Alfalfa would therefore be able to facilitate soil moisture and soil N levels, shelter the newly planted seedlings from damage, as well as reduce the ground exposure to wind and water erosion, without having competitive effects beyond the first growing season. Moreover, for integrated purposes, selection of a lower profile legume that would not interfere with light penetration, but could still provide ground cover and N-fixation may produce better results for aspen growth. This however, would negate any potential facilitated reduction in the level of damage to the tree seedlings.

Conversely, early growth of aspen has limited potential for integrated production with marsh reedgrass. Although marsh reedgrass was associated with reduced aspen damage rates in the first year after planting, it was otherwise an aggressive and persistent competitor. Marsh reedgrass was associated with lower levels of available soil NO_3-N and soil water. This translated to significant reductions in aspen size with a trend towards greater intensity of competitive interference in comparison to alfalfa. Because of the rhizomatous root network and increased tillers and total plant mass each year, competition would continue to intensify with time. As previous empirical and experimental evidence has suggested, management to displace or replace marsh reedgrass cover would have positive effects on aspen seedling growth. Moreover, the positive effects of marsh reedgrass control would be realized with a minimal loss in potential facilitating effects, independent of its importance in natural conditions where its value for wildlife or ecosystem function may take precedence.

The application of these data should be tempered by other factors affecting competition and facilitation in operational situations. Specifically, the rigid spatial distribution and constant density used in this experiment do not reflect many potential field situations. Forage seeding in agroforests is more likely to produce a random plant arrangement at a greater density. This could potentially intensify or diminish the competitive balance with aspen seedlings. Reducing the interplant distance may increase competitive interference through greater root or canopy overlap. Conversely a greater density may either increase or decrease competition intensity, as well as alter facilitative mechanisms. Increasing alfalfa density could increase root distribution around the aspen seedlings, thus intensifying competition for soil resources, but also increasing the dispersion of N additions. Alternately, by increasing density, total alfalfa biomass may remain constant, but with individual plant sizes reduced through intraspecific competition. These shorter alfalfa would interfere less with PAR reaching the aspen stem, thus decreasing above-ground competition.

Table 3-1 Aspen (*Populus tremuloides* Michx.) seedling growth in monoculture and mixtures with either alfalfa (*Medicago sativa* L.) or marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) at a fixed density. Values listed are the least-squares means (adjusted standard error). Means in the same row followed by the same letter are not significantly different ($p>0.05$).

		Competitor	
Focal Aspen Response	**Aspen Monoculture**	**Alfalfa**	**Marsh Reedgrass**
Diameter			
Growth 2001 (mm)	3.3 (0.5) a	2.0 (0.5) a	2.1 (0.5) a
Growth 2002 (mm)	4.7 (0.5) a	1.9 (0.5) b	1.7 (0.5) b
RGR$_D$ 2001	0.8 (0.1) a	0.4 (0.1) b	0.5 (0.1) b
RGR$_D$ 2002	0.7 (0.1) a	0.3 (0.1) b	0.3 (0.1) b
Height			
Growth 2001 (cm)	15.0 (3.7) a	7.9 (3.7) b	16.9 (3.7) a
Growth 2002 (cm)	34.6 (3.7) a	14.7 (3.7) b	14.5 (3.9) b
RGR$_H$ 2001	0.4 (0.2) a	0.2 (0.2) a	0.6 (0.2) a
RGR$_H$ 2002	0.6 (0.2) a	0.3 (0.2) a	0.6 (0.2) a
Leaf Number			
2001	58 (40) a	61 (40) a	75 (41) a
2002	431 (40) a	217 (40) b	210 (43) b
Leaf Area (cm^2)	2961 (306) a	1138 (306) b	713 (317) b
Area Per Leaf (cm^2)	6.7 (0.4) a	4.4 (0.4) b	3.2 (0.4) c
Leaf mass (g)	19.2 (2.6) a	6.8 (2.6) b	4.3 (2.6) b
Stem mass (g)	26.3 (4.2) a	12.5 (4.2) b	6.3 (4.2) b
Shoot mass (g)	45.5 (6.7) a	19.4 (6.7) b	12.6 (6.7) b

Table 3-2 Intensity and importance of alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) competition for aspen (*Populus tremuloides* Michx.) seedling growth. Values listed are the least-squares means (adjusted standard error). Means in the same row, within the same measure, followed by * are significantly different (p<0.05).

	Intensity of Competition		**Importance of Competition**	
	Alfalfa	**Marsh Reedgrass**	**Alfalfa**	**Marsh Reedgrass**
Diameter				
Growth 2001 (mm)	1.4 (0.5)	1.3 (0.5)	-0.8 (0.4)	0.2 (0.4) *
Growth 2002 (mm)	2.8 (0.5)	3.0 (0.5)	-1.8 (0.4)	-1.8 (0.4)
Height				
Growth 2001 (cm)	7.1 (3.7)	-1.9 (3.7) *	-0.9 (0.3)	-0.8 (0.3)
Growth 2002 (cm)	19.9 (3.7)	20.1 (3.9)	-1.6 (0.3)	-1.7 (0.3)
Leaf Number				
2001	-3 (44)	15 (44)	-6.6 (1.5)	-7.7 (1.6)
2002	214 (44)	250 (47)	-3.2 (1.5)	-4.0 (1.6)
Leaf Area (cm^2)	1766 (306)	2191 (317)	-3.4 (0.6)	-4.2 (0.6)
Area Per Leaf (cm^2)	2.3 (0.4)	3.5 (0.4) *	-2.0 (0.3)	-3.0 (0.3) *
Leaf mass (g)	12.2 (2.6)	14.6 (2.6)	4.0 (1.2)	2.3 (1.2)
Stem mass (g)	13.1 (4.2)	17.4 (4.2)	7.9 (2.1)	4.8 (2.2)
Shoot mass (g)	27.0 (4.9)	32.1 (4.9)	-6.7 (1.6)	-9.0 (1.7)

Table 3-3 Relationship of aspen (*Populus tremuloides* Michx.) growth and size to the proportion of open sky photosynthetically active radiation (PAR) intercepted, soil moisture (SM) at four dates, available nitrate (NO_3-N), available ammonium (NH_4-N) and surrounding plant mass (Mass) in 2002.

Dependent Variable	**Adjusted Model R^2**	**Independent Variable**	**Partial R^2**	**Model R^2**	**B#**	**Prob > |T|***
RGR_D **	0.58	PAR	0.39	0.39	0.006	<0.01
		SM, July 15	0.10	0.49	0.07	0.05
		SM, July 2	0.09	0.58	-0.05	0.04
		SM, June 10	0.07	0.65	0.04	0.05
Leaf Number	0.43	SM, May 28	0.19	0.19	25.5	0.03
		NH_4	0.11	0.30	-12.1	0.07
		Mass	0.11	0.41	-0.5	0.05
		SM, July 15	0.05	0.52	54.7	0.04
Area per Leaf (APL)	0.62	SM, July 15	0.53	0.53	0.51	<0.01
		Mass	0.08	0.62	-0.004	0.03
Leaf Area	0.50	SM, May 28	0.24	0.24	240.5	0.01
		SM, July 15	0.17	0.41	453.5	0.03
		Mass	0.15	0.56	-3.8	<0.01
Shoot Mass	0.53	SM, July 15	0.19	0.19	10.71	0.02
		NO_3	0.17	0.36	2.35	0.02
		Mass	0.13	0.49	-0.04	0.07
		NH_4	0.08	0.57	-1.54	0.06

Regression Coefficient.

* Probability of the T-test of whether inclusion of this variable improves the overall fit of the regression model.

** Relative diameter growth

Table 3-4 Above-ground net primary production (ANPP) of alfalfa (*Medicago sativa* L.) and marsh reedgrass (MRG) (*Calamagrostis canadensis* (Michx.) Beauv.) in fixed-density mixtures with aspen (*Populus tremuloides* Michx.) seedlings. Values listed are the least-squares means (adjusted standard error). Means in the same row followed by the same letter are not significantly different ($p>0.05$). ANPP of monocultures in bold font for emphasis.

	Alfalfa in Focal Position			MRG in Focal Position		
Competitor:	**Aspen**	**Alfalfa**	**MRG**	**Aspen**	**Alfalfa**	**MRG**
Focal plant mass (g)						
2001	335 (38) a	**238 (41)** b	202 (38) b	13 (38) c	4 (38) c	**43 (41)** c
2002	257 (39) a	**175 (41)** b	131 (38) b	46 (38) cd	9 (39) c	**90 (41)** d
Total ANPP (g m^{-2})						
2001		**801 (55)** a	346 (55) c		632 (55) b	**217 (58)** d
2002		**691 (55)** a	462 (55) c		563 (55) b	**452 (58)** bc

Table 3-5 Marsh reedgrass (MRG) (*Calamagrostis canadensis* (Michx.) Beauv.) tiller number and tiller mass in fixed-density mixtures with either aspen (*Populus tremuloides* Michx.) seedlings or alfalfa (*Medicago sativa* L.). Values listed are the least-squares means (adjusted standard error). Means followed by the same letter in the same row are not significantly different (p>0.05).

	Aspen Competitor		Alfalfa Competitor		Marsh Reedgrass Monoculture	
Tiller Number						
2001	30 (11)	a	8 (11)	a	97 (12)	b
2002	97 (11)	a	19 (11)	b	195 (12)	c
Tiller Mass (g)						
2001	0.41 (0.04)	a	0.41 (0.04)	a	0.47 (0.05)	a
2002	0.54 (0.04)	a	0.45 (0.05)	a	0.47 (0.05)	a

Table 3-6 Relative yield totals of above-ground net primary production of fixed-density mixtures of aspen (*Populus tremuloides* Michx.) seedlings, alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.). Values listed are the least-squares means (adjusted standard error). Means followed by the same letter are not significantly different (p>0.05).

Focal Plant	Competitor	Relative Yield Total		
Aspen	Alfalfa	1.00	(0.08)	a
	Marsh Reedgrass	0.90	(0.09)	ab
Alfalfa	Aspen	0.86	(0.08)	ab
	Marsh Reedgrass	0.92	(0.08)	ab
Marsh reedgrass	Aspen	0.65	(0.08)	b
	Alfalfa	0.74	(0.08)	b

Figure 3-1 Focal arrangement of plants in plots.

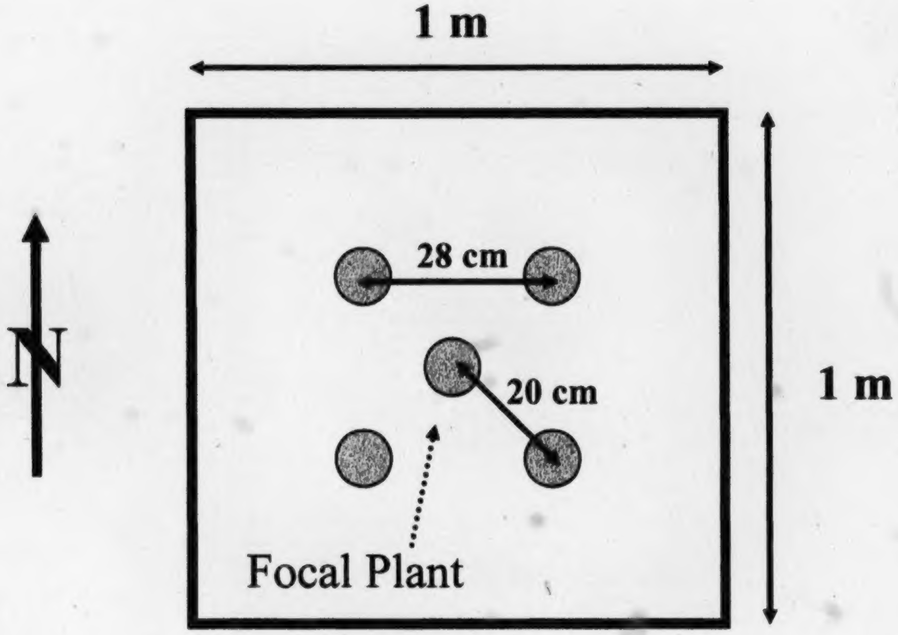


Figure 3-2 Growing season precipitation at the University of Alberta's Ellerslie Research Station from 2000 to 2002.

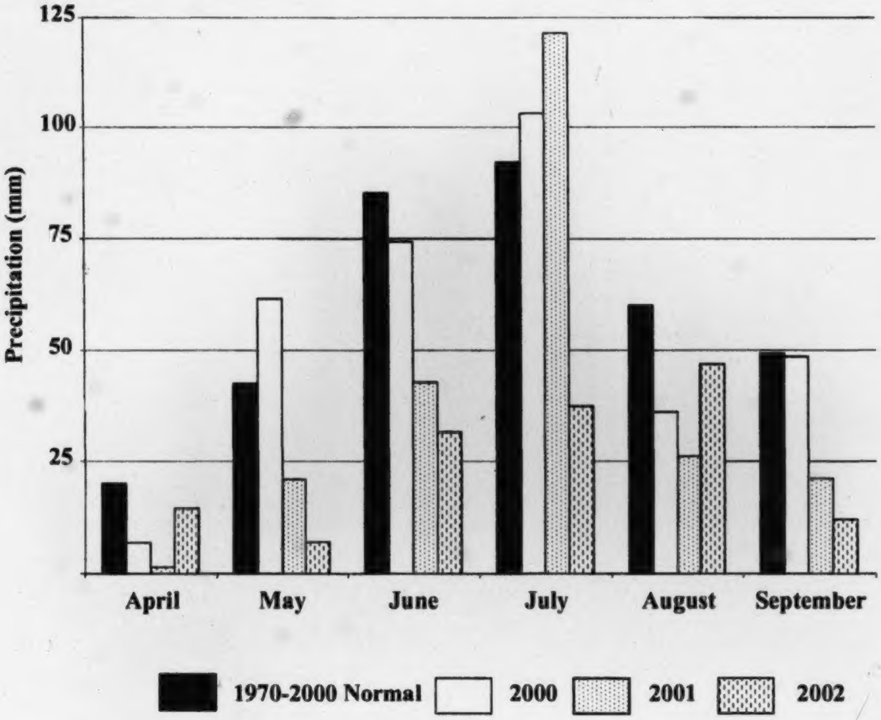


Figure 3-3 Volumetric moisture content in upper 15-cm of soil under fixed-density mixtures of aspen (*Populus tremuloides* Michx.) seedlings, alfalfa (*Medicago sativa* L.) and marsh reedgrass (MRG) (*Calamagrostis canadensis* (Michx.) Beauv.) in 2002. Vertical lines indicate the adjusted standard error of the least squares means.

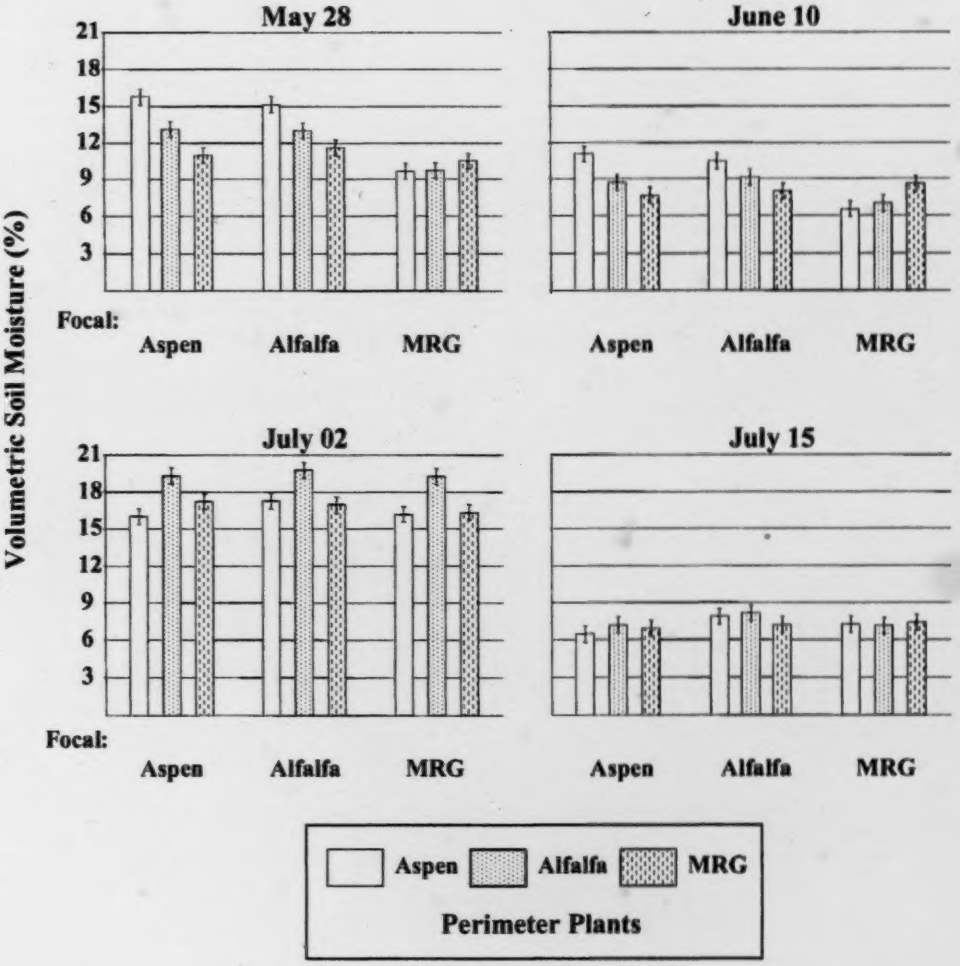


Figure 3-4 Exchangeable nitrate (NO_3-N) and ammonium (NH_4-N) in upper 15-cm of soil under fixed-density mixtures of aspen (*Populus tremuloides* Michx.) seedlings, alfalfa (*Medicago sativa* L.) and marsh reedgrass (MRG) (*Calamagrostis canadensis* (Michx.) Beauv.) in July 2002. Vertical lines indicate the adjusted standard error of the least squares means.

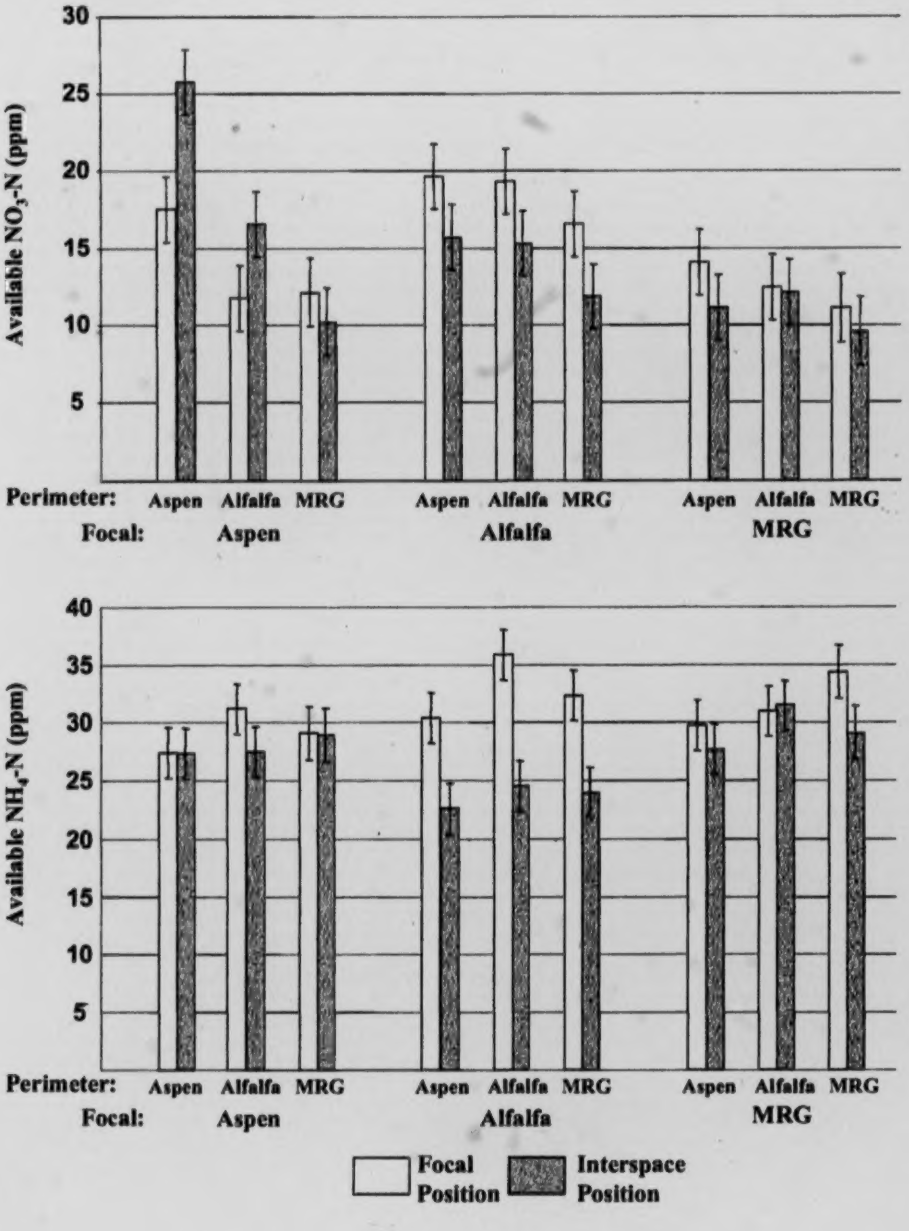


Figure 3-5 Root mass concentration (mg cm^{-3} soil) in the upper 15-cm of soil at two plot positions in fixed-density mixtures of aspen (*Populus tremuloides* Michx.) seedlings, alfalfa (*Medicago sativa* L.) and marsh reedgrass (MRG) (*Calamagrostis canadensis* (Michx.) Beauv.) in July 2002. Vertical lines indicate the adjusted standard error of the least squares means.

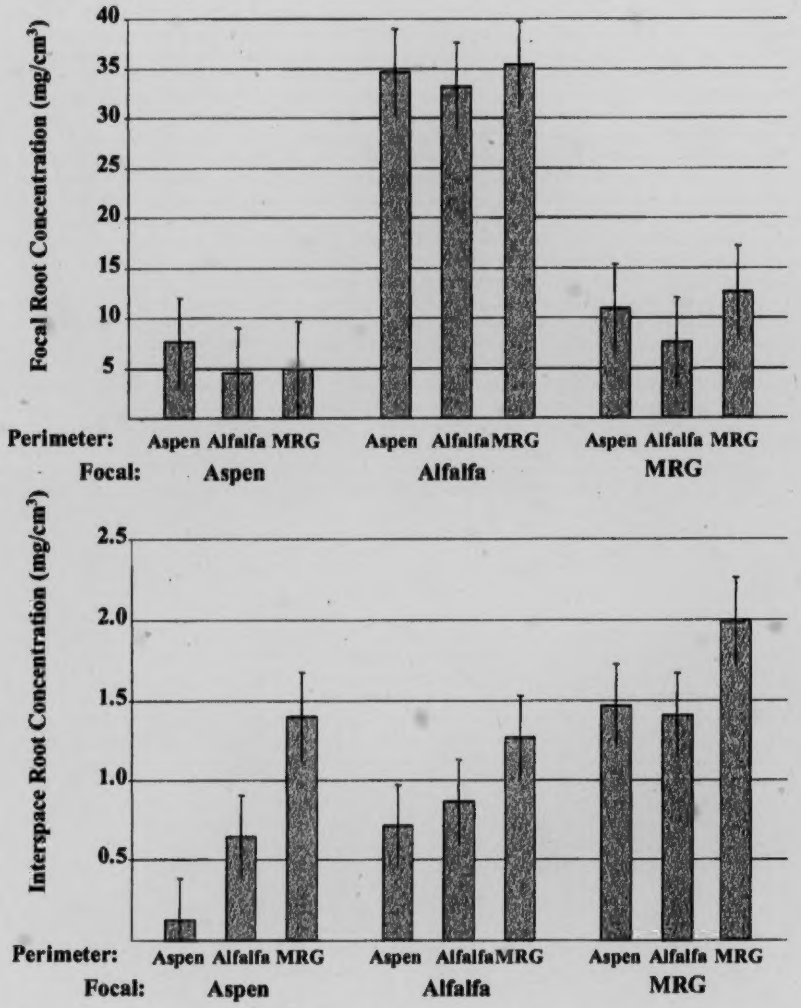
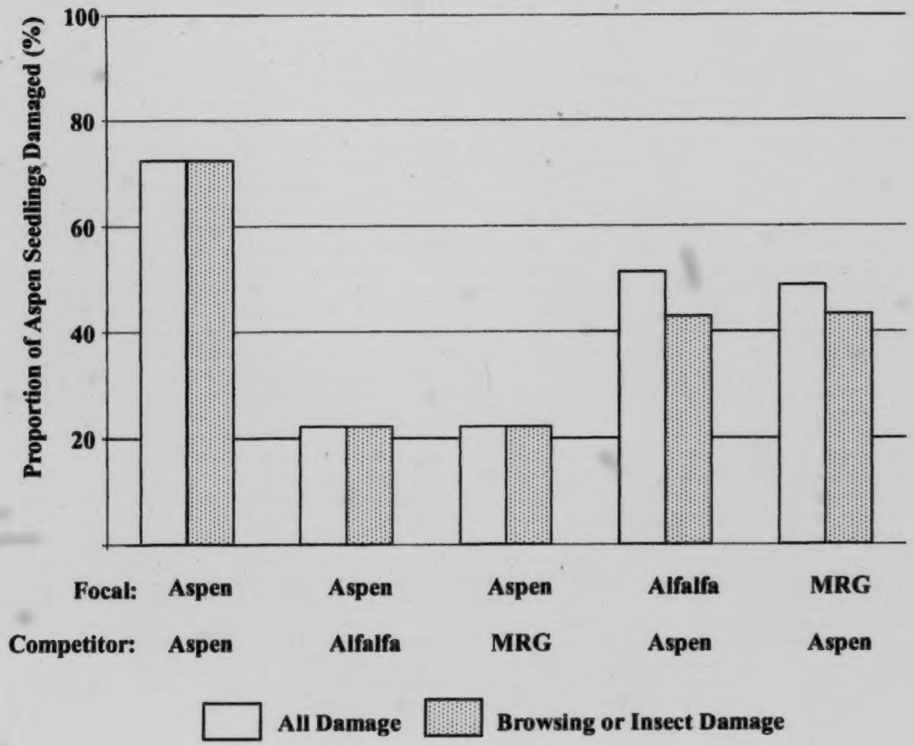


Figure 3-6 Aspen (*Populus tremuloides* Michx.) seedling damage in the first year of growth in monoculture and mixtures with alfalfa (*Medicago sativa* L.) and marsh reedgrass (MRG) (*Calamagrostis canadensis* (Michx.) Beauv.).



3.5 Literature Cited

Atsatt, P.R. and D.J. O'Dowd. 1976. Plant defense guilds. Science 193: 24-29.

Bailey, A.W, and R.K. Gupta. 1973. Grass – woody plant relationships. Canadian Journal of Plant Science 53: 671-676.

Balatinecz, J.J., D.E. Kretschmann and A. Leclercq. 2001. Achievements in the utilization of poplar wood – guideposts for the future. The Forestry Chronicle 77: 217-392.

Callaway, R.M. and L.R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958-1965.

Carlson, D.H., S.H. Sharrow, W.H. Emmingham and D.P. Lavender. 1994. Plant-soil-water relations in forestry and silvopastoral systems in Oregon. Agroforestry Systems 25: 1-12.

Chamblee, D.S. 1972. Relationships with other species in a mixture. Chapter 10, pp 211-228 *in*: Hansen, C.H. (editor). Alfalfa Science and Technology. Agronomy Number 15. American Society of Agronomy, Madison, WI, 812 p.

Daubenmire, R. 1959. A canopy coverage method of vegetational analysis. Northwest Science 33: 43-61.

Haines, S.G., L.W. Haines and G. White. 1978. Leguminous plants increase sycamore growth in Northern Alabama. Soil Science Society of America Journal 42: 130-132.

Jolliffe, P.A. 1988. Evaluating the effects of competitive interference on plant performance. Journal of Theoretical Biology 130: 447-459.

Landhäusser, S.M. and V.J. Lieffers. 1998. Growth of *Populus tremuloides* in association with Calamagrostis canadensis. Canadian Journal of Forest Research 28:396-401.

Littell, R.C., W.W. Stroup and R.J. Freund. 2002. SAS® for Linear Models, Fourth Edition. SAS Institute Inc., Cary, NC, 466 p.

Maynard, D.G. and Y.P. Kalre. 1993. Nitrate and exchangeable ammonium nitrogen. Chapter 4, pp 25-38 *in*: Carter, M.R. (editor) Soil Sampling and Methods of Analysis. Canadian Society of Soil Science, Lewis Publisher, Boca Raton, FL, 823 p.

Nambiar, E.K.S. and R. Sands. 1993. Competition for water and nutrients in forests. Canadian Journal of Forest Research 23: 1955-1968.

Pearson, H.A., M.L. Elliott-Smith, A. Martin Jr., and V.C. Baldwin. 1994. Subterranean clover: nutrients for pines. Pages 17-20 *in*: Symposium on Current Research in the Chemical Sciences: Third Annual Southern Station Chemical Sciences Meeting. General Technical Report SO-101, USDA, Forest Service, Southern Forest Experiment Station, New Orleans, LA.

Rivard, P.G., P.M. Woodward and R.L. Rothwell. 1990. The effect of water table depth on white spruce (*Picea glauca*) seedling growth in association with the marsh reed grass (*Calamagrostis canadensis*) on wet mineral soil. Canadian Journal of Forest Research 20: 1553-1558.

Schroth, G. 1999. A review of belowground interactions in agroforestry, focusing on mechanisms and management options. Agroforestry Systems 43: 5-34.

Strong, W.L. and K.R. Leggat. 1992. Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife, Edmonton, AB, 59 p.

Trowbridge, R. and F.B. Holl. 1992. Early growth of lodgepole pine after establishment of alsike clover-*Rhizobium* nitrogen-fixing symbiosis. Canadian Journal of Forest Research 22: 1089-1093.

Vandermeer, J. 1989. Ecology of Intercropping. Cambridge University Press, New York, 223 p.

Walton, P.D. 1983. Production and Management of Cultivated Forages. Reston Publishing Company, Inc., Reston, Virginia. p 240.

Ward, B. 2001. Poplar as a crop – It's place in a changing agriculture. *In:* Schroeder, W. and J. Kort (editors). Temporate Agroforestry: Adaptive and Mitigative Roles in A Changing Physical and Socio-Economic Climate. Proceedings of the seventh biennial conference on agroforestry in North America, August 13-15, 2001, Regina, Saskatchewan, pp 9 –11.

Welden, C.W. and W.L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Quarterly Review of Biology 61: 23-44.

Wojtkowski, P. 1998. The Theory and Practice of Agroforestry Design. Science Publishers Inc., Enfield, NH, 282 p.

CHAPTER 4

Root and Shoot Effects in Mixtures of Aspen Seedlings, Alfalfa and Marsh Reedgrass

4.1 Introduction

Interactions between aspen (*Populus tremuloides* Michx.) stands and their understory can be complex mixtures of negative (competition) and positive (facilitation) processes (Callaway and Walker 1997), with both above- and below-ground components. Mature aspen dominate the use of light and their large clonal root networks are effective at foraging for soil moisture and nutrients. Aspen seedlings however, can experience intense competition with co-dominant vegetation for both light and soil-based resources. Plants do not compete for light without simultaneously competing for water and nutrients (Cannell and Grace 1993). However, in accordance with Liebig's (1840) law of the minimum, the factor in least supply should most limit growth. In plant mixtures, competition for light has frequently been assumed to dominate interspecific interactions, with growth of individuals proportionate to their interception of light (Montieth 1977). Competition for water and nutrients, however, may be equally or more important in accounting for yield differences. Agroforestry systems are designed to optimize the biological returns from mixtures of trees and herbaceous crops and therefore, require an understanding of ecological processes to ensure manipulations of the system enhance facilitation and/or minimize competition.

It can be difficult experimentally to separate the effects of light from those of water and nutrients through plant removal. Plants with large leaf areas intercept large amounts of light and also use large amounts of soil resources. Removing plants to assess their effect on neighbouring vegetation therefore simultaneously increases light, water and nutrient availability (Cannell and Grace 1993). To overcome this problem, above- and below-ground processes have been separated by selectively removing shoot or root influences with partitions. With this approach, the foliage of neighbouring plants can remain intermixed (and presumably competing for light), while the roots of each plant are separated by a below-ground barrier (reducing or eliminating root effects), and vice versa. Across species and habitats these studies have produced varied outcomes. The majority of evidence however, suggests that below-ground competition generally controls plant productivity. For example, root-based competition was the dominant interaction in 23 greenhouse studies where the effects of root competition were separated from shoot competition (Wilson 1988). Likewise, 40 of 47 root trenching studies in forest ecosystems reviewed reported a positive response in plant species released from root effects (Coombs and Grubb 2000).

Aspen shoot and root growth are strongly correlated, and rapid juvenile growth depends on effective root foraging (Pregitzer and Friend 1996). Aspen with poorly developed root systems are susceptible to competition for water and nutrients with understory vegetation because their lateral roots are concentrated in the upper 5-20 cm of soil (Pregitzer and Friend 1996). Removal of root-based competition therefore, should have positive effects on aspen seedling growth and survival. Indeed, prior research has demonstrated improved aspen seedling growth in tundra plantings when competition was reduced by root trenching and a below-ground barrier (Hobbie and Chapin 1998). There are also indications however, that herbaceous vegetation plays an important, positive role in organic matter and nutrient cycling in aspen stands (Perala and Alban 1982, Ruark 1990). Moreover, in the soil nutrient complex, nitrogen (N) is the most important factor regulating aspen root growth (Pregitzer and Friend 1996). Nitrogen fixed and released by a legume could therefore promote aspen growth. Elimination of below-ground effects may also block facilitation between aspen and surrounding species, but must be balanced against the competitive effects from the presence of other species. In these situations, increasing water or nutrients (by irrigation or fertilization) may be more beneficial to aspen growth than eliminating surrounding herbaceous vegetation.

This experiment employed above-and below-ground partitions to selectively minimize interactions of alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) surrounding solitary aspen seedlings. Marsh reedgrass is a common, often dominant, boreal and sub-boreal species that can impede aspen development because of its competitive nature. It is a strong competitor for soil moisture and nutrients, with up to 80% of its root mass concentrated in the upper

10 cm of the soil (Rivard *et al.* 1990). Under controlled conditions, marsh reedgrass suppressed aspen sucker growth directly through root-based competition, and indirectly through the effects of its leaf litter (Landhäusser and Lieffers 1998).

Alfalfa is one of the most widely grown forage crops in the world and can form symbiotic associations with the N-fixing bacteria *Rhizobium meliloti.* Under good growing conditions alfalfa is capable of fixing in excess of 150 kg N ha^{-1} yr^{-1} (Walton 1983). Fixed N becomes available for uptake by other vegetation when alfalfa leaf litter and root nodules break down and release nutrients into the soil. Moreover, tap-rooted varieties of alfalfa are able to access deep soil profiles and thus, can potentially minimize surface competition for moisture and nutrients. However, modern alfalfa cultivars have been bred for rapid, vigorous growth and can competitively suppress other vegetation. To date, N transfer from a legume to aspen has not been documented, although a positive carryover effect of soil enriched from a N-fixing shrub has been demonstrated (Bailey and Gupta 1973).

4.2 Objectives and Hypotheses Tested

The objectives of this experiment were to isolate and compare above- and below-ground processes between aspen seedlings, alfalfa and marsh reedgrass. The following null hypotheses were tested:

1. Alfalfa and marsh reedgrass roots have no below-ground effects on aspen seedling mass, root concentration, leaf area, height or root-collar diameter;
2. Alfalfa and marsh reedgrass shoots have no above-ground effects on aspen seedling mass, root concentration, leaf area, height or root-collar diameter; and,
3. Alfalfa and marsh reedgrass above- and below-ground effects do not interact to influence aspen seedling mass, root concentration, leaf area, height and root-collar diameter.

4.3 Methods

Research Site

Research was conducted on field plots at the University of Alberta's Ellerslie Research Station in Edmonton, Alberta (53° 25' N, 113° 33' W). The station is situated in the Aspen Parkland ecoregion (Strong and Leggat 1992) and has a continental climate characterized by cold winters and short, warm summers (1970-2000 normal January and July temperatures are -14 and 16 °C, respectively). Ellerslie receives 460 mm of precipitation annually with approximately 70% during the May to September growing season. Plots were on a deep, silt-clay-loam, Orthic Black Chernozemic soil that has been cultivated with a variety of crops for approximately 50 yr.

Treatments and Experimental Design

Aspen seedlings, alfalfa and marsh reedgrass were established in 210, 1-m^2 plots. Plants were arranged with an aspen seedling centered in the middle of the plot and either four plants of the other two species equidistantly spaced in a cross-pattern with a 20-cm spacing from the aspen, or no surrounding vegetation. Partitions were used to selectively separate plant roots and shoots, creating four treatment combinations:

1. full root and shoot effects (no partitions);
2. no root effects (below-ground partition separating aspen and herbaceous roots);
3. no shoot effects (above-ground partition separating herbaceous shoot material from aspen stems); and,
4. no root or shoot effects (both types of partitions in place).

Each possible combination of the three species mixtures with root and shoot partition treatments were replicated 10 times and randomly assigned to their plot locations. Due to aspen mortality during planting, one complete treatment combination (aspen without surrounding vegetation, with both types of partitions in place) was dropped from the experiment so that the aspen could be used to fill the specified number of replicates for other treatments. One additional replicate set of plots without vegetation but with root barriers in place was established in 2002 to monitor the effects of the root exclusion tubes alone on soil moisture. All plots were hand-weeded throughout the experiment as needed to maintain only the prescribed vegetation in each plot. A 5-m perimeter buffer was established around the outside of the plots to minimize the risk of agri-chemical drift from adjacent cropping activities. The perimeter was mowed occasionally to minimize edge-effects for the experimental plots.

Alfalfa (cv 'Nordica') was established from seed inoculated with a coating of *Rhizobium meliloti* bacteria in May 2000. Additional plants were established at the same time outside of the experimental plot area to provide alfalfa plants of the same age as those in the experimental units for fill-planting. Because of sporadic germination and mortality due to both wind-driven soil particles and defoliation by insects, approximately 90% of the alfalfa planting failed during the first year. Replacements were transplanted on four occasions during the establishment year, of which the latter two transplantations were to replace previous transplants that did not survive. During each transplantation, 100 ml of water was applied to all alfalfa plants (i.e. both newly transplanted and established plants). A small number of plants were replaced due to over-winter mortality, in May 2001 coinciding with the aspen planting.

Marsh reedgrass was established from rhizomes in June 2000. Rhizomes were collected the previous day from the Blackfoot Provincial Grazing Reserve (53° 30' N, 113° 03' W), south of Elk Island National Park, Alberta in a Aspen Parkland-Boreal ecoregion transition zone. Rhizomes were cut into 5-cm segments, with each containing a live tiller node. Rhizome segments were planted 2-cm deep with the tiller node oriented towards the surface, and were watered with 100 ml at the time of planting. Approximately 50% of rhizomes sprouted and established marsh reedgrass plants by the end of the first growing season. Surviving plants were excavated in May 2001 at the time of aspen planting and divided into equal-sized tussocks of 10 to 12 tillers each, which were subsequently replanted to fill all the prescribed marsh reedgrass experimental locations.

Aspen seedlings from a common seed lot (1+0 bare root stock) were planted in May 2001. Aspen that died during the first 2 weeks after planting were replaced, after which no plant replacement was conducted. All plots were irrigated over a three week period in May and early June 2001 to counter the effects of low precipitation during the establishment of aspen seedlings and newly transplanted alfalfa and marsh reedgrass plants. In total, the equivalent of 65.4 mm of precipitation was applied, or approximately equal to the 30-yr normal for this period. Aspen seedlings, alfalfa and marsh reedgrass were grown together through 2 growing seasons (May 2001 to July 2002).

Root barriers consisted of 18-cm diameter by 40-cm long, plastic pipe buried vertically such that the upper lip of the tubing was flush with ground-level. Aspen seedlings were planted into the centre of the tubes as prescribed. Above-ground partitions were constructed from thin, plastic netting (1-mm thick in 1-cm by 1-cm mesh). The netting had minimal interference on precipitation and light penetration; direct measurement found 95% of photosynthetically active radiation (PAR) penetrated the netting. On the prescribed plots, a 90- by 100-cm sheet of netting was anchored to the ground at four attachment points that horizontally dissected the middle of the plot in a north-south line. The four corners of the netting were stretched and suspended 20-cm above the ground on wire supports, creating a north-south oriented, v-shaped zone around the aspen seedling free of other vegetation. New herbaceous growth into this zone was moved periodically (weekly or more frequently, as necessary) by detaching the corner supports of the netting and gently pushing the new plant material to the outside of the partition before reattaching the corners.

Measures

Direct measures of PAR were made at the approximate peak standing crop of the herbaceous species in each year. In 2001, measures were taken in early August with a Decagon AccuPAR™ ceptometer; in 2002, a LICOR, LI-190SA™ quantum sensor was used just prior to the termination of the experiment in mid-July. In each year, PAR sampling was conducted under clear-sky conditions, over a 1- to 2-hr period around solar noon. The relative amount of PAR reaching the mid-point of aspen seedlings at each sampling period was calculated by comparing measures taken within a few seconds of each other at the mid-height of the aspen and above each plot with an unobstructed sky view. Volumetric soil moisture in the upper 15-cm soil layer of each plot was recorded in 2002 at 3 week intervals with a Delta-T™ theta probe. Soil moisture readings were taken at two locations in each plot. One measure was made inside the root exclusion tubes, and the second approximately 15-cm from the plot centre in the same randomly pre-determined direction from the aspen, outside of the root barrier tubes (or at the corresponding distances from the aspen stems on plots without below-ground barriers). Daily precipitation and air temperatures were recorded with a Campbell Scientific CR10™ weather station located 0.5 km from the research plots.

Monthly assessments of aspen damage and survival were conducted during the growing seasons of 2001 and 2002. Aspen damage was assessed visually and the proportion of each seedling damaged estimated on a scale from 1 to 6, corresponding to the classes developed for ocular assessment of plant canopy cover (Daubenmire 1959). Plants were designated as "dead" when no green leaf or stem material was visible.

Baseline measures of aspen height (to the nearest 0.5 cm), root-collar diameter (to the nearest 1 mm) and the number of leaf buds were measured at the time of planting. Aspen height and diameter were measured again at the end of the first growing season (after aspen leaf-fall), the following spring (after initiation of new leaf growth) and at the termination of the experiment in July 2002. Relative height growth (RGR_H) and relative diameter growth (RGR_D) were determined each year by dividing the change in each measure from beginning to end of each year, by the measure at the beginning of the year. The number of fully-formed aspen leaves on each seedling was recorded prior to leaf-fall in 2001 and at the termination of the experiment in 2002. At the end of the experiment aspen stems were cut from their roots at the root crown and leaves and stems separated. Leaf area was measured directly with a LI-COR, LI-3100™ area meter, on a randomly selected subsample of 50 leaves from each aspen seedling (or less if the total number of leaves on a given tree did not exceed 50). Area per leaf (APL) was estimated by dividing the total leaf area by the number of leaves used in the leaf area measurement. Leaf area per tree was estimated by multiplying APL by the number of leaves per tree. Leaves and stems were dried at 70 °C to constant mass, and weighed to the nearest 0.01 g.

Above-ground net primary production (ANPP) of the alfalfa and marsh reedgrass were estimated by clipping plant material off at ground level in September 2001 and at the termination of the experiment in July 2002. Samples were dried at 70 °C to constant mass, and weighed to the nearest 0.01 g.

Following harvest of above-ground plant material at the end of the experiment, five, 15-cm deep soil cores were extracted from each plot. Within the root exclusion tubes (or corresponding location) a single 7.6-cm diameter core was collected (the "inside" samples), and four, 3.8-cm diameter cores were collected at the mid-point between the aspen seedling and each perimeter plant (or corresponding location) and combined (the "outside" samples). Volumes of the inside and composite of the outside samples were equivalent (684 cm^3). All soil samples were separated from the air-dried soil cores by screening the contents through a 2-mm Canadian Standard Sieve.

Roots were separated from the soil cores in a three-phase process. First, remaining fine soil particles were washed from the root cores with low pressure through a 1.70-mm Canadian Standard Sieve. Sieve contents were then floated in a container of clean water and extraneous material discarded. The remaining material was strained through a piece of fabric, with recovery of root segments by hand. Root content was not separated by species and all roots recovered for a given sample were dried together at 70 °C to constant mass, and weighed to the nearest 0.01 g. Root mass concentration was calculated by dividing the root mass in each soil core by the soil core volume.

Available nitrate (NO_3-N) and ammonium (NH_4-N) were determined by atomic absorption with a spectrophotometer after extraction from the soil with a 5:1 mixture with 2 *M* KCl (Maynard and Kalre 1993). Exchangeable phosphate-phosphorous (PO_4-P) and calcium (Ca) were extracted using the ammonium acetate method at pH 7.0 (Hendershot *et al.* 1993). The concentration of exchangeable cations was determined from atomic absorption of the ammonium acetate extracts.

Total, above- and below-ground competitive responses were calculated for aspen height and diameter growth, RGR_H, RGR_D, leaf number, leaf area, APL, and the mass of all plants (Cahill 2002, Appendix 1). Competition intensity was also calculated for these variables as the difference in aspen growth without surrounding vegetation to that with either alfalfa or marsh reedgrass present. Importance of competition to aspen growth relative to differences due to damage was calculated from the ratio of competition intensity to the difference between undamaged and damaged trees for each aspen measure (Welden and Slauson 1986, Appendix 1). For the purposes of these calculations, "optimal" growth was defined as the growth of aspen in the absence of surrounding vegetation.

Analyses

Differences in aspen survival and damage were tested with Chi-square analyses of the counts between treatment groups. Damage patterns in the aspen were compared to aspen size using a Kruskal-Wallis test of the rank-sums. Analyses of end measures of aspen mass and leaf area, root mass concentration, and soil nutrients (Tables A2-5 and A2-6, Appendix 2) were conducted with mixed linear models for a completely random design (Littell *et al.* 2002). Annual measures of PAR, aspen growth, ANPP of the herbaceous species, indices of competition based on these measures, as well as periodic measures of soil moisture in 2002 were analyzed with mixed linear models for repeated measures with a completely random design (Tables A2-7 and A2-8, Appendix 2). A compound symmetry covariance model was used in the repeated measures analyses. This model was selected iteratively for each response variable by testing several structures and comparing Schwarz's Bayesian information criterion. This criterion test is based on the maximum likelihood fit corrected for the number of parameters in the model, analogous to the adjusted R^2 employed in multiple regression analyses. Species composition, root and shoot partitions were assumed to have fixed effects and the variation between plots (assessed with replication) was assumed to introduce random effects. A Kenward-Roger correction was applied to the degrees of freedom to eliminate sample size bias. Data were checked for normality and equality of variances and most were found to meet these criteria for parametric analyses. Square-root transforms were conducted on NO_3-N, NH_4-N and PO_4-P data, and soil moisture data were transformed with a natural logarithm to obtain normal distributions of the respective residual errors.

Differences between specific treatment combinations were separated with individual degree of freedom contrasts when necessary.

Aspen growth measures were regressed against surrounding vegetation biomass, PAR, soil moisture, and soil nutrients. Regressions of multiple independent variables were conducted using both forward stepwise and backward elimination techniques to find the combination and order of variables that produced the best-fit models. Simple linear regressions were also conducted of soil moisture and nutrient levels correlated to the respective root mass concentrations in each plot position. Plots of the residual values from the regression equations against their expected values indicated linear models were appropriate for the analyses.

4.4 Results and Discussion

Weather and Photosynthetically Active Radiation

This study was conducted during three dry years, each progressively more arid. Total annual precipitation was approximately 433, 266 and 215 mm from 2000 to 2002, respectively, all below the annual (1970-2000) normal of 460 mm. Likewise, April to September (inclusive) precipitation in 2000, 2001 and 2002 was 95, 71 and 64%, respectively, of the 30-yr normal for this period (Figure 3-1, Chapter 3). Conditions were particularly dry during the early part of the 2002 growing season (April to June), when only 37% of the normal amount of precipitation fell. Moreover, precipitation distribution patterns diverged from normal in 2000 and 2001. Early growing season precipitation was generally lower than normal, followed by above-average rainfall in July, creating early season droughts in each of those years. Mean monthly temperatures were generally within the expected range for these periods, with the exception of June and July, 2002, when temperatures exceeded the long-term normals by 20 and 27%, respectively.

Predictably, less PAR reached the mid-point of aspen surrounded by either herbaceous species than those grown alone (Figure 4-1). Alfalfa intercepted the most PAR in both years ($p<0.0001$), reducing levels to less than 40% of open sky conditions in 2001, almost double the amount intercepted by marsh reedgrass. In 2002, alfalfa intercepted more than 80% of incident PAR. Marsh reedgrass PAR interception increased in 2002; however it still only intercepted less than half the amount of alfalfa. Above-ground partitions functioned as planned, as PAR levels with partitions in place did not differ ($p=0.89$) from control aspen without surrounding vegetation in either year.

Soil Nutrients and Moisture

With the exception of NO_3-N, soil nutrient levels at experiment-end were unaffected by the treatments. Available NH_4-N, exchangeable PO_4-P and Ca averaged 29.5 ± 0.5 ppm, 0.73 ± 0.03 ppm, and 25.8 ± 0.2 meq 100 g^{-1}, respectively, and did not differ ($p>0.10$) with species present, shoot separation or plot position. Both herbaceous species, however, did substantially reduce 'outside' NO_3-N ($p<0.0001$) in comparison to unvegetated controls (Figure 4-2). On average, NO_3-N levels were slightly greater with alfalfa ($p=0.05$) than marsh reedgrass. Competitive partitioning of the soil NO_3-N was also evident, as separation of roots increased ($p=0.02$) NO_3-N inside the root exclusion tubes in plots of either herbaceous species (Figure 4-2). The effects of alfalfa and marsh reedgrass on inside NO_3-N did not differ ($p=0.10$). In the control plots without herbaceous vegetation, outside NO_3-N levels with or without the root barriers were almost double the amount inside, and placement of the root barrier on the control plots did not affect ($p=0.10$) 'inside' NO_3-N. The outside amount around the solitary aspen with root barriers in place reflects the levels available in the absence of plant uptake. Because these levels did not differ from plots of solitary aspen with no root barrier in place, it demonstrates that aspen made little use of the N pool outside the immediate zone around the seedling.

Available NH_4-N ($p=0.23$), exchangeable PO_4-P ($p=0.60$) and Ca ($p=0.68$) did not correlate to root mass concentrations, and NO_3-N showed a very weak relationship ($R^2=0.02$, $p=0.04$) to the same. Furthermore, soil NO_3-N, NH_4-N and Ca all had very small ($R^2<0.09$) roles in explaining variation in aspen growth (Table 4-5).

Soil moisture levels varied ($p<0.0001$) with sampling period in 2002 (Figure 4-3). Overall, levels declined from May to early July as minimal precipitation fell in this period. A single 24-mm rainfall prior to the 2 July sampling temporarily elevated soil moisture levels, followed by drought conditions and very warm air temperatures (maximums >27 °C), which amplified soil water depletion. Across sampling dates, species ($p<0.0001$) and the separation of root ($p<0.0001$) and shoot ($p=0.01$) effects influenced soil moisture levels (Figure 4-3). The effects of the herbaceous species and root partitioning, however, varied ($p<0.0001$) within sampling periods. Moreover, the effects of shoot partitioning interacted with root separation treatments. Across sampling periods, herbaceous shoots increased ($p=0.01$) soil moisture when shoots were intermixed and root barriers were also in place, but did not affect soil moisture when below-ground effects were also present. This suggests that herbaceous canopies increased soil moisture by blocking evaporation, but concomitant root uptake by the herbs when present negated this increase.

Competition was evident from the soil moisture patterns on 28 May and 10 June. Separation of roots during that time with surrounding alfalfa or marsh reedgrass resulted in greater soil moisture levels inside the barriers than outside (Figure 4-3). Conversely, the root barriers around aspen without accompanying herbaceous vegetation resulted in lower soil moisture levels inside the tubes than outside from 10 June to the termination of the experiment on 15 July, and reflects soil water use by the aspen. Species differences manifested during the 28 May sampling. In that period soil moisture levels at both plot positions with roots mixed were lowest ($p=0.01$) in the presence of marsh reedgrass, greatest without herbaceous vegetation and intermediate with alfalfa. With roots separated, the same differences were evident, with the exception that levels inside the barriers were equivalent to aspen controls with no surrounding vegetation. The lowest soil moisture levels recorded occurred on the final sampling date (15 July) with full root and shoot interactions from marsh reedgrass. The greatest soil moisture levels were observed inside root exclusion tubes after the early July rainfall, with either alfalfa or marsh reedgrass shoots mixed with the aspen. Of those two, soil water content under aspen surrounded by marsh reedgrass were slightly greater ($p<0.01$) than aspen mixed with alfalfa, possibly due to greater canopy interception of precipitation by the alfalfa.

Despite the relationship of soil moisture levels to below-ground effects, root mass concentrations correlated poorly ($R^2=0.05$, $p<0.01$) to 28 May moisture levels, coincident with the only period in which soil moisture differed significantly between all species combinations, and did not ($p>0.20$) relate to soil moisture at any other date.

Root Mass Concentrations

Across species, there were greater root concentrations ($p<0.0001$) in the plot centres than the plant interspaces (Figure 4-4). Root mass concentrations in the inside position were greatest ($p=0.02$) for aspen without competing vegetation, and marginally lower with either alfalfa or marsh reedgrass competition. Outside root mass concentrations were greatest ($p=0.03$) with the presence of marsh reedgrass and lowest with the solitary aspen. Root separation did not ($p=0.08$) affect root mass concentrations except for control plots of aspen without competing vegetation ($p<0.0001$). Control plot differences resulted from the fact that the only roots present on those plots were inside the root exclusion tubes. Shoot interactions only influenced root mass concentration ($p=0.05$) on marsh reedgrass plots, and the nature of the difference varied ($p=0.03$) by plot position (Figure 4-4). With aspen and marsh reedgrass roots mixed, inside root mass concentrations were greater with the shoots separated. A substantial portion of the inside root mass concentration on these plots appeared to be marsh reedgrass rhizomes. Separation of the marsh reedgrass foliage from the aspen stem allowed greater solar input, hence soil warming, at the plot center. This could have promoted marsh reedgrass rhizome growth into this area and account for the root mass differences. With below-ground barriers in place, separation of the aspen and marsh reedgrass shoots resulted in decreased outside root mass concentrations. The same phenomenon working in reverse may have produced this result. Separation of the shoots was accomplished by using netting to divert shoots from the centre of the plots towards the edges. This effectively increased foliar cover in the outside positions, which would have blocked solar input to the soil and hence deterred marsh reedgrass rhizome growth.

Interference of Root Treatments on Aspen Growth

Although root barriers of the same type and similar size used in this experiment have been used to successfully separate below-ground effects among herbaceous species

(Cahill 2002), the root tubes interfered with the normal development of aspen and restricted all aspects of seedling growth (Table 4-1 to 4-4). Aspen seedlings planted into the root exclusion tubes had less diameter growth ($p<0.0001$) and lower RGR_D ($p<0.0001$) (Table 4-1), less height growth ($p<0.0001$) and lower RGR_H ($p<0.001$) (Table 4-2), fewer leaves ($p<0.0001$), with less leaf area per tree ($p<0.0001$) and APL ($p<0.0001$) than those grown without tubes (Table 4-3). Moreover, the mass of aspen leaves ($p<0.0001$), stems ($p<0.0001$) and shoots ($p<0.0001$) were all lower with root barriers in place (Table 4-4). Reduced aspen growth with root barriers is also evident in the competitive response ratios (Table 4-6). Below-ground competitive response (BCR) for all but RGR_D indicates up to 400% better aspen growth with full root interactions.

Root tubes likely did not restrict movement of soil resources to the aspen, but more probably changed aspen root morphology creating trees with less growth potential. The only soil nutrient affected by root separation was NO_3-N, and its levels were increased inside some of the root separation treatments. Likewise, soil moisture levels either did not differ or were greater inside the tubes than outside when both herbaceous competitors were present and root barriers were in place (Figure 4-3). Furthermore, soil moisture levels were equivalent ($p>0.10$) inside and outside of the empty root exclusion tubes in all sampling periods in 2002, indicating the untapped soil moisture did not differ under the influence of the root barriers. Root mass concentrations in the plot centres were equivalent in the aspen controls with and without root barriers (Figure 4-4). However, with the root barriers absent, lateral roots extended radially from aspen into the rest of the plot creating a larger soil foraging area. These differences in aspen root morphology were observed after soil cores were extracted from the plots. Aspen within the root tubes were not 'root-bound' but did lack long (>10-cm) lateral surface roots. Therefore, aspen did not outgrow the tubes, but rather, a change in rooting pattern caused by the tubes blocking lateral root extension may have created 'bonsai' effects; smaller versions of the un-barriered aspen. This also explains the paradoxical results of the regressions of environmental variables to aspen growth. Of the variables tested, soil moisture levels at various dates consistently, and counter-intuitively, were negatively associated with aspen growth (see correlation coefficients, Table 4-5). This can be explained by the fact that root barriers had positive effects on resources and negative effects on aspen growth. Root separation increased soil water surrounding the aspen seedlings, but this was coupled with the negative effects of the tubes on aspen growth resulting from changes in aspen root distribution patterns. Hence the net negative effect of the root barriers gives the appearance of a negative effect of soil water availability on aspen growth.

Because the separation of below-ground effects between aspen and herbaceous species was confounded by changes in aspen root morphology caused by the root barriers, further discussion of the impacts on aspen growth will be limited to above-ground effects and species differences.

Aspen Growth and Competitive Response

The control group of aspen seedlings had much greater growth than those with surrounding vegetation. All aspects of aspen size and growth (Tables 4-1 to 4-4) were larger ($p<0.001$) in this treatment than those with surrounding herbaceous vegetation, except RGR_H ($p=0.14$). Separation of herbaceous shoots from aspen stems increased diameter growth ($p=0.03$, Table 4-1), leaf area ($p<0.0001$, Table 4-3), leaf mass ($p<0.0001$), stem mass ($p<0.01$) and total shoot mass ($p<0.001$) (Table 4-4). Conversely, RGR_D ($p=0.08$), height growth ($p=0.92$), RGR_H ($p=0.41$), leaf number ($p=0.41$) and APL ($p=0.15$) were all unaffected by shoot separation.

Alfalfa ANPP was greater ($p<0.0001$) than that of marsh reedgrass in both years. Alfalfa ANPP averaged 772 ± 53 and 531 ± 53 g m^{-2}, in 2001 and 2002, respectively, whereas marsh reedgrass produced 179 ± 54 and 351 ± 53 g m^{-2} in those years. Notably, while alfalfa production decreased from 2001 to 2002 in concert with drought conditions, marsh reedgrass ANPP nearly doubled in that period, indicating greater drought tolerance in the otherwise shallow-rooted marsh reedgrass. None of the aspen measures correlated ($p>0.10$) to PAR availability at peak above-herbaceous standing crop, but a negative relationship with ANPP of competing plants did explain some of the variation in aspen growth. Indeed, of the multiple variables tested, competitor ANPP factored significantly ($p<0.07$) in all of the aspen growth measures (Table 4-5) except RGR_H in 2002.

Moreover, competitor ANPP was the sole factor of significance correlating to aspen diameter growth across both years ($R^2=0.23$, $p<0.0001$), RGR_D across both years ($R^2=0.22$, $p<0.0001$), height growth across both years ($R^2=0.08$, $p<0.0001$), RGR_H across both years ($R^2=0.02$, $p=0.03$), leaf number across both years ($R^2=0.06$, $p<0.001$) and total leaf area per tree ($R^2=0.35$, $p<0.0001$). For regressions conducted on 2002 variables, competitor ANPP explained the most variability (partial $R^2=0.20$ to 0.37, $p<0.001$) of the measures tested (Table 4-5).

Competitive response values indicate that independent of root barrier effects, aspen diameter and height growth in both years, the number of leaves, APL and total leaf area per tree in 2002, and all measures of aspen mass were competitively reduced by marsh reedgrass shoots (Table 4-6). Similarly, alfalfa competitively reduced aspen diameter, as well as leaf, stem and total shoot mass through its above-ground effects. The relative importance of shoot interactions to total competitive response unfortunately cannot be unambiguously separated from the confounding negative influence of the root barrier treatment on the same.

Damage was not relevant to aspen height or diameter growth in 2001 given that damaged trees grew better than undamaged trees in the first year after aspen planting (see negative values, Table 4-7). In 2002, independent of shoot separation, competition from surrounding species had 2.7 to 3.2 times more impact on aspen height growth, and 2.7 to 3.7 times more impact on diameter growth than the influence of damage (Table 4-7). Moreover, the importance of competition for height growth did not vary with shoot separation ($p=0.79$) or species ($p=0.43$), suggesting the effects were tied to the presence of the herbaceous species, but not specifically to interference with PAR reaching the aspen stem. Competition was slightly less important for aspen diameter growth in the presence of marsh reedgrass than alfalfa when the shoots were separated ($p<0.001$) in 2002. Leaf numbers were also influenced to the greatest extent by competition, but were unaffected ($p>0.15$) by separation of the herbaceous shoots from the aspen stem in either year. Similarly, competition was more important than damage effects for aspen APL, but was somewhat less important ($p<0.01$) in the marsh reedgrass plots when shoots were separated. Leaf, stem and total shoot mass were also influenced to a greater extent by shoot competition from the herbaceous species. Conversely, damage was more important to aspen leaf area per tree than competitive effects, with the two species having different effects resulting from the separation of shoot material ($p<0.0001$). Separation of alfalfa shoots from aspen increased the ratio slightly towards greater importance of competition (0.2 to 0.3), whereas with marsh reedgrass the opposite was true.

Damage and Survival

A chemical deterrent (Deer-Away™) successfully prevented browsing damage to aspen until a very large rainfall in 2001 (60 mm over 48 hours) apparently reduced the effectiveness of the chemical treatment, after which 18% of aspen were browsed over the ensuing week. Following this damage, all research plots were enclosed with a 2-m tall, paige-wire fence, after which no additional browsing occurred. Prior to fencing, aspen grown without surrounding vegetation had greater browsing damage ($p<0.001$, $n=106$) than when grown with adjacent alfalfa or marsh reedgrass. Greater than half of the aspen without surrounding vegetation were browsed in 2001, whereas only 21 and 15% of aspen surrounded by alfalfa and marsh reedgrass were browsed, respectively. Herbaceous vegetation may have hidden aspen from visual detection by deer, or may have provided a more palatable or preferable alternative to aspen seedlings in side-by-side choices, thus providing direct and indirect protection for trees.

Importance of competition ratios (Table 4-7) provided conflicting evidence with respect to the sheltering effects of herbaceous vegetation. Damage directly reduced aspen leaf area and was more important than competition in explaining differences in aspen leaf area with either herbaceous species present. If herbaceous species sheltered aspen from damage, separation of herbaceous shoots should have increased exposure of aspen to greater damage and therefore increased the importance of damage relative to competition (reflected in a smaller importance of competition ratio). This was the case for marsh reedgrass (decreasing from 0.3 to 0.2) but not with alfalfa (increasing from 0.2 to 0.3).

Alternatively, browsing damage patterns evident may be confounded by differences in tree size. Aspen grown without competitors had superior growth rates and it is possible that larger trees may have been more susceptible to damage. Using both diameter ($p<0.0001$) and height ($p=0.01$) as the metric for aspen size, a rank-sum analysis indicated damaged aspen were 26 and 17% larger, respectively than undamaged seedlings. However, because diameter and height were only recorded at the beginning and end of the growing season, and most of the damage occurred during the middle of the growing period, it is unclear if size differences had been expressed at the time of the damage or resulted from the damage.

Very little additional damage occurred during the over-winter period following the first growing season (6% of aspen), and despite ubiquitous, small-scale insect feeding on the leaves in the second growing season, only 18% of trees had substantial damage (>5% of leaf area) in that period and damage patterns did not differ between treatments ($p=0.28$, $n=105$). Nor did damage influence aspen survival. Indeed, after the final transplantations in early June 2001, 96% of the aspen survived to the end of the experiment and there were no differences ($p=0.37$) in survival due to damage, root or shoot separation, nor from species combinations.

Conclusions and Management Implications

Both above- and below-ground ecological processes were evident in the early dynamics of aspen-herbaceous species mixtures. Unfortunately, unintended interference of the below-ground barriers with aspen root development limited assessment of aspen growth parameters to the resource levels observed. However, several trends give insight into the root and shoot dynamics of these species mixtures. Shoot effects can be determined directly from the data and some below-ground effects can also be inferred from differences in soil resources measured in 2002. Surrounding herbaceous vegetation reduced soil water, available NO_3-N, and PAR. Moreover, competitor ANPP correlated negatively with most aspects of aspen growth. Net competition was expressed in most aspects of tree seedling growth, although survival was not affected. The competition observed also incorporated density effects because aspen without neighbouring vegetation would have had a growth advantage with fewer plants per unit area. Nevertheless, these conditions replicate operational situations where land managers can choose whether or not to establish or control vegetation surrounding trees planted at fixed density.

Differences between the two herbaceous species were primarily related to individual plant sizes. Alfalfa were larger and intercepted more PAR, however, this was generally not significantly associated with variation in aspen growth. In absolute terms, marsh reedgrass depleted soil water levels to the lowest levels and proportionate to ANPP, marsh reedgrass was a more aggressive competitor. For example, despite having a much larger biomass to support, NO_3-N levels were slightly greater with alfalfa ($p=0.05$) than marsh reedgrass. This may have been due to less NO_3-N depletion by alfalfa, through N additions to the soil from decaying alfalfa roots or leaf litter, or a combination of the two.

Soil NO_3-N in these agricultural soils were greatest in the absence of herbaceous uptake, however this may only be a short-term phenomenon. Without inputs of organic matter or N, available soil N will very likely decrease through time, and may fall below optimal levels for aspen growth. Moreover, as evidenced by the similar levels of available NO_3-N around solitary aspen with or without root barriers, aspen did not draw significantly from the 'outside' NO_3-N pool. Without the presence of vegetation between trees this could lead to N-leakage from the system with a net loss that may have to be replaced at a future date. Herbaceous species draw on this N and incorporate it into their biomass, lowering soil N, but retaining higher overall system N. Nitrogen bound in this vegetation would be released back into the system when the tree canopy closes and suppresses understory growth. Surrounding vegetation may also reduce soil temperature, which can reduce N losses by preventing volatilization of ammonia (He *et al.* 1999). Thus, there may be some merit in balancing the short-term competitive effects from the presence of herbaceous species against longer-term negative effects on soil fertility. The positive role of herbaceous ground cover could also be amplified through its role in reducing wind and water erosion. Moreover, N-fixing legumes could further enhance long-term N availability, and data in this study shows a trend towards increased N with the presence of alfalfa.

Although other soil nutrients were not influenced by the interaction of these three species, herbaceous species may be important in the long-term retention and cycling of nutrients. For example, aspen understory vegetation produced 19% of the total above-ground litter biomass, but contributed 36% of the litter N, 40% of the litter P, and 59% of the litter K (Perala and Alban 1982). Similarly, Ruark (1990) found that understory vegetation represented 14, 24 and 13% of the available pools of P, K and magnesium (Mg), respectively, in a young aspen forest.

Further research into below-ground competitive partitioning among tree seedlings and surrounding vegetation is needed to definitively identify the importance of root and shoot interactions. In retrospect, the method employed in this experiment was not suitable for testing the effects on aspen or other species with similar rooting patterns due to its effects on lateral root development. Increasing the diameter of the root exclusion tube however, would unlikely improve the functionality of this design. The below-ground barriers utilized in this study were sufficient to increase soil water and NO_3-N inside the tubes to levels equivalent to aspen without surrounding vegetation. Moreover, increasing the diameter of the root barrier would also increase the minimum distance from the aspen seedling that competing vegetation could be established. Beyond a certain distance this would confound separation of the shoot treatments because separation of the rooting points with a large diameter tube would effectively separate the shoots as well.

Table 4-1 Above- and below-ground effects of alfalfa (*Medicago sativa* L.) and marsh reedgrass (MRG) (*Calamagrostis canadensis* (Michx.) Beauv.) on aspen (*Populus tremuloides* Michx.) seedling diameter growth and relative diameter growth (RGR_D). Values listed are the least-squares means (adjusted standard error).

Root Effects	**Shoot Effects**	**Competitor**	**Diameter Growth (mm)**				**RGR_D**			
			2001		**2002**		**2001**		**2002**	
Mixed	Mixed	None	3.3	(0.4)	5.0	(0.4)	0.7	(0.1)	0.7	(0.1)
		Alfalfa	2.0	(0.4)	1.9	(0.4)	0.4	(0.1)	0.3	(0.1)
		MRG	2.1	(0.4)	1.7	(0.4)	0.5	(0.1)	0.3	(0.1)
	Separated	None	4.8	(0.4)	5.7	(0.4)	1.0	(0.1)	0.7	(0.1)
		Alfalfa	1.9	(0.4)	2.0	(0.4)	0.4	(0.1)	0.3	(0.1)
		MRG	2.6	(0.4)	3.1	(0.4)	0.5	(0.1)	0.4	(0.1)
Separated	Mixed	None	2.0	(0.4)	2.6	(0.4)	0.4	(0.1)	0.4	(0.1)
		Alfalfa	1.1	(0.4)	1.2	(0.4)	0.2	(0.1)	0.2	(0.1)
		MRG	1.5	(0.4)	0.5	(0.4)	0.3	(0.1)	0.1	(0.1)
	Separated	Alfalfa	1.9	(0.4)	1.6	(0.4)	0.4	(0.1)	0.3	(0.1)
		MRG	2.0	(0.4)	1.4	(0.4)	0.4	(0.1)	0.3	(0.1)

Table 4-2 Above- and below-ground effects of alfalfa (*Medicago sativa* L.) and marsh reedgrass (MRG) (*Calamagrostis canadensis* (Michx.) Beauv.) on aspen (*Populus tremuloides* Michx.) seedling height growth and relative height growth (RGR_H). Values listed are the least-squares means (adjusted standard error).

Root Effects	**Shoot Effects**	**Competitor**	**Height Growth (cm)**				**RGR_H**			
			2001		**2002**		**2001**		**2002**	
Mixed	Mixed	None	13.7	(3.1)	32.3	(3.1)	0.4	(0.1)	0.6	(0.1)
		Alfalfa	7.9	(3.1)	14.7	(3.1)	0.2	(0.1)	0.3	(0.1)
		MRG	16.9	(3.1)	15.0	(3.3)	0.6	(0.1)	0.6	(0.1)
	Separated	None	15.8	(3.0)	34.1	(3.0)	0.5	(0.1)	0.6	(0.1)
		Alfalfa	11.3	(3.0)	12.3	(3.0)	0.4	(0.1)	0.3	(0.1)
		MRG	14.1	(3.0)	16.8	(3.0)	0.4	(0.1)	0.3	(0.1)
Separated	Mixed	None	9.2	(3.1)	11.9	(3.1)	0.2	(0.1)	0.3	(0.1)
		Alfalfa	8.7	(3.0)	12.6	(3.0)	0.3	(0.1)	0.4	(0.1)
		MRG	6.1	(3.0)	4.6	(3.0)	0.2	(0.1)	0.1	(0.1)
	Separated	Alfalfa	6.6	(3.1)	8.3	(3.1)	0.2	(0.1)	0.2	(0.1)
		MRG	8.4	(3.0)	7.9	(3.0)	0.3	(0.1)	0.2	(0.1)

Table 4-3 Above- and below-ground effects of alfalfa (*Medicago sativa* L.) and marsh reedgrass (MRG) (*Calamagrostis canadensis* (Michx.) Beauv.) on aspen (*Populus tremuloides* Michx.) seedling leaf number, leaf area and area per leaf. Values listed are the least-squares means (adjusted standard error).

Root Effects	Shoot Effects	Competitor	Leaf Number 2001		Leaf Number 2002		Leaf Area (cm^2)		Area Leaf $^{-1}$ (cm^2)	
Mixed	Mixed	None	65	(38)	403	(38)	3040	(221)	8.1	(0.4)
		Alfalfa	73	(38)	230	(38)	991	(221)	4.3	(0.4)
		MRG	45	(38)	216	(40)	755	(235)	3.2	(0.4)
	Separated	None	67	(36)	527	(36)	4339	(210)	8.5	(0.3)
		Alfalfa	61	(36)	220	(36)	1144	(210)	4.9	(0.3)
		MRG	81	(36)	361	(36)	1822	(210)	4.4	(0.3)
Separated	Mixed	None	57	(36)	255	(38)	1376	(221)	5.4	(0.4)
		Alfalfa	56	(36)	184	(36)	873	(210)	4.4	(0.3)
		MRG	66	(36)	145	(36)	502	(210)	3.9	(0.3)
	Separated	Alfalfa	66	(38)	194	(38)	765	(221)	3.9	(0.4)
		MRG	67	(36)	179	(36)	673	(210)	4.3	(0.3)

Table 4-4 Above- and below-ground effects of alfalfa (*Medicago sativa* L.) and marsh reedgrass (MRG) (*Calamagrostis canadensis* (Michx.) Beauv.) on aspen (*Populus tremuloides* Michx.) seedling mass. Values listed are the least-squares means (adjusted standard error).

Root Effects	Shoot Effects	Competitor	Leaf Mass (g)		Stem Mass (g)		Shoot Mass (g)	
Mixed	Mixed	None	23.2	(2.4)	17.2	(2.1)	40.7	(4.4)
		Alfalfa	6.2	(2.4)	11.4	(2.1)	17.6	(4.4)
		MRG	4.8	(2.6)	9.2	(2.2)	14.0	(4.6)
	Separated	None	36.2	(2.3)	29.4	(2.0)	65.6	(4.1)
		Alfalfa	10.2	(2.3)	7.0	(2.0)	17.2	(4.1)
		MRG	21.1	(2.4)	13.6	(2.1)	34.7	(4.4)
Separated	Mixed	None	11.2	(2.4)	9.0	(2.1)	20.2	(4.4)
		Alfalfa	5.4	(2.3)	2.8	(2.0)	8.1	(4.1)
		MRG	3.9	(2.3)	2.1	(2.0)	5.9	(4.1)
	Separated	Alfalfa	6.0	(2.4)	4.2	(2.1)	10.1	(4.4)
		MRG	5.1	(2.3)	3.4	(2.0)	8.5	(4.1)

Table 4-5 Relationship of aspen (*Populus tremuloides* Michx.) growth and size to soil moisture (SM) at four dates, available nitrate (NO_3-N), available ammonium (NH_4-N), exchangeable calcium (Ca) and surrounding plant mass (Mass) in 2002.

Variable	Model R^2	Independent Variable	Partial R^2	Model R^2	B#	Prob > |T|*
Height Growth	0.25	Mass	0.20	0.20	-0.02	<0.01
		SM, July 2	0.04	0.24	-1.05	<0.01
		NO_3	0.03	0.27	0.13	0.06
Diameter Growth	0.40	Mass	0.37	0.37	-0.001	<0.01
		SM, July 2	0.05	0.42	-0.16	<0.01
RGR_D	0.37	Mass	0.31	0.31	-0.001	<0.01
		SM, July 2	0.06	0.37	-0.03	<0.01
		NO_3	0.02	0.39	0.003	0.06
Leaf Number	0.25	Mass	0.22	0.22	-0.39	<0.01
		NH_4	0.03	0.25	4.76	0.05
		SM, July 15	0.03	0.28	-14.05	0.06
Area per Leaf (APL)	0.44	Mass	0.32	0.32	-0.004	<0.01
		Ca	0.09	0.41	0.26	<0.01
		SM, June 15	0.03	0.44	0.14	0.07
		NO_3	0.02	0.46	0.02	0.06
Leaf Mass	0.37	Mass	0.36	0.36	-0.3	<0.01
		NH_4	0.02	0.38	2.5	0.06
Stem Mass	0.33	Mass	0.28	0.28	-0.02	<0.01
		SM, July 15	0.05	0.33	-1.91	0.05
Shoot Mass	0.37	Mass	0.34	0.34	-0.05	<0.01
		SM, July 15	0.03	0.37	-1.42	0.05
		NH_4	0.02	0.39	0.44	0.06

* Probability of the T-test of whether inclusion of this variable improves the overall fit of the regression model.

# Regression coefficient.

Table 4-6 Competitive response ratio of above- and below-ground effects of alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) on aspen (*Populus tremuloides* Michx.) seedling growth.

	With Alfalfa Competitor			With Marsh Reedgrass Competitor		
Aspen Response	**ACR**[*]	**BCR**[+]	**TCR**[#]	**ACR**	**BCR**	**TCR**
Root Collar Diameter						
Growth 2001 (mm)	0.58	1.01	1.06	0.75	1.30	1.06
Growth 2002 (mm)	0.77	1.29	1.21	0.36	2.21	1.25
RGR_D 2001	0.53	0.95	0.91	0.84	1.20	1.25
RGR_D 2002	0.68	0.99	0.91	0.41	1.59	1.02
Height						
Growth 2001 (cm)	1.32	1.72	1.20	0.73	1.68	2.02
Growth 2002 (cm)	1.51	1.47	1.76	0.58	2.15	1.91
RGR_H 2001	1.34	1.72	1.04	0.77	1.24	2.11
RGR_H 2002	1.79	1.23	1.47	0.64	1.33	2.64
Leaf Number						
2001	1.25	1.36	1.64	1.20	1.19	1.45
2002	0.95	1.13	1.87	0.81	2.01	1.21
Leaf Area (cm^2)	1.14	1.49	1.30	0.75	2.71	1.12
Area Per Leaf (cm^2)	1.12	1.25	1.09	0.92	1.03	0.75
Leaf mass (g)	0.90	1.71	1.04	0.77	4.16	0.95
Stem mass (g)	0.66	1.67	2.74	0.60	3.95	2.67
Shoot mass (g)	0.80	1.69	1.74	0.70	4.08	1.65

[*] Above-ground competitive response.
[+] Below-ground competitive response.
[#] Total competitive response.

Table 4-7 Importance of above-ground competition from alfalfa (*Medicago sativa* L.) or marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) for aspen (*Populus tremuloides* Michx.) seedling growth relative to damage. Values listed are the least-squares means (adjusted standard error). Optimal growth of aspen defined from controls without surrounding vegetation.

	With Alfalfa Competitor		With Marsh Reedgrass Competitor	
Aspen Response	**Shoots Mixed**	**Shoots Separate**	**Shoots Mixed**	**Shoots Separate**
Root Collar Diameter				
2001	-1.5 (0.3)	-1.3 (0.3)	-1.2 (0.3)	-0.9 (0.3)
2002*	3.3 (0.3)	3.1 (0.3)	3.7 (0.3)	2.7 (0.3)
Height				
2001	-4.8 (1.4)	-4.2 (1.4)	-1.9 (1.4)	-2.2(1.4)
2002	2.7 (1.4)	3.1 (1.4)	3.2 (1.4)	2.9 (1.4)
Leaf Number				
2001	1.5 (0.8)	1.2 (0.8)	0.5 (0.8)	2.7 (0.8)
2002	2.0 (0.8)	1.9 (0.8)	2.6 (0.8)	1.2 (0.8)
Leaf Area * #	0.2 (0.02)	0.3 (0.02)	0.3 (0.02)	0.2 (0.02)
Area Per Leaf	4.2 (0.3)	4.1 (0.3)	5.0 (0.3)	4.2 (0.3)
Leaf mass #	2.3 (0.2)	2.2 (0.2)	1.5 (0.2)	1.7 (0.2)
Stem mass	1.8 (0.2)	2.1 (0.2)	2.1 (0.2)	1.7 (0.2)
Shoot mass #	2.7 (0.2)	2.4 (0.2)	2.9 (0.2)	1.7 (0.2)

* Main effect for shoot separation significant ($p<0.01$)
# Main effect for species significant ($p<0.01$)

Figure 4-1 Influence of alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) shoots on the proportion of open-sky photosynthetically active radiation (PAR) reaching aspen (*Populus tremuloides* Michx.) seedlings at peak herbaceous standing crop in 2001 and 2002.

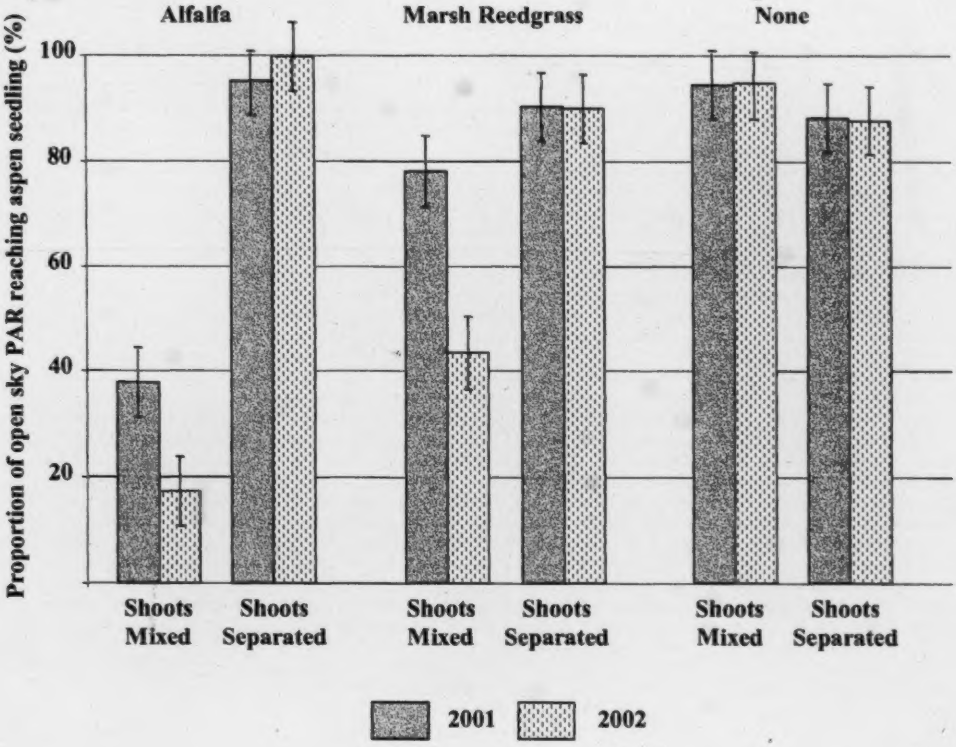


Figure 4-2 Root and shoot effects of alfalfa (*Medicago sativa* L.), marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) and aspen (*Populus tremuloides* Michx.) seedlings on available nitrate (NO_3-N) in the upper 15-cm of soil, July 2002. "Inside" samples from within root exclusion tubes or corresponding distance from aspen on plots without below-ground barrier. "Outside" samples from interspace between aspen and surrounding vegetation, outside of root exclusion tubes or corresponding distance from aspen on plots without below-ground barrier. *Shoots of surrounding vegetation intermixed with aspen stem (S). **Shoots of surrounding vegetation separated from aspen stem (NS).

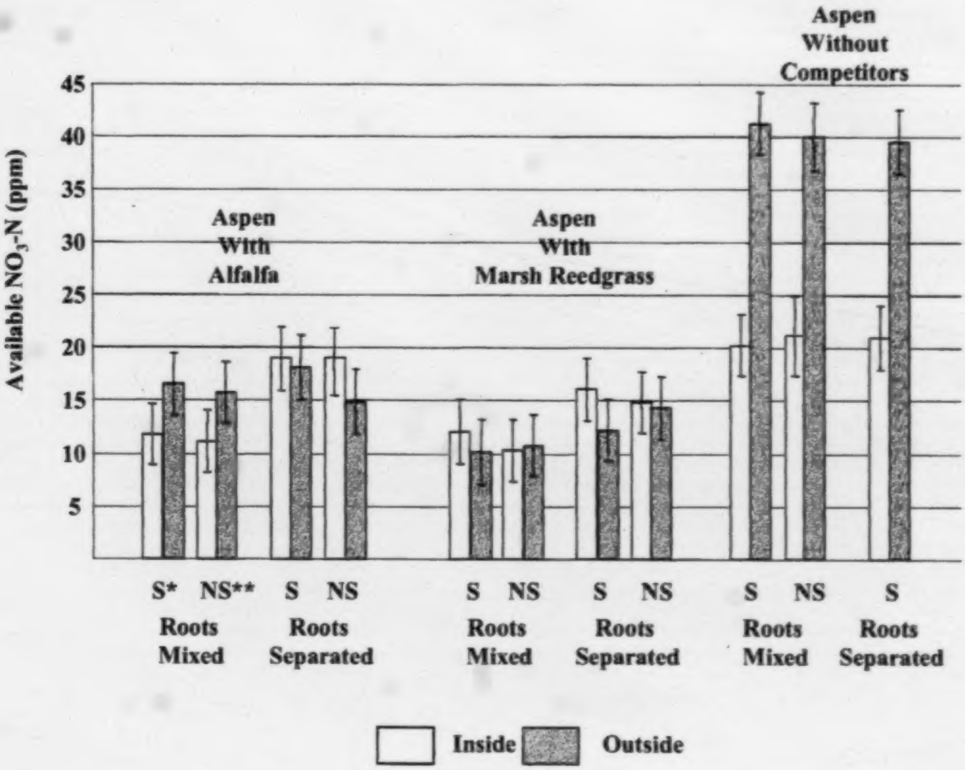


Figure 4-3 Root and shoot effects of alfalfa (*Medicago sativa* L.), marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) and aspen (*Populus tremuloides* Michx.) seedlings on volumetric soil moisture in the upper 15-cm of soil at four dates in 2002. "Inside" samples from within root exclusion tubes or corresponding distance from aspen on plots without below-ground barrier. "Outside" samples from interspace between aspen and surrounding vegetation, outside of root exclusion tubes or corresponding distance from aspen on plots without below-ground barrier. *Shoots of surrounding vegetation intermixed with aspen stem (S). ⁺Shoots of surrounding vegetation separated from aspen stem (NS).

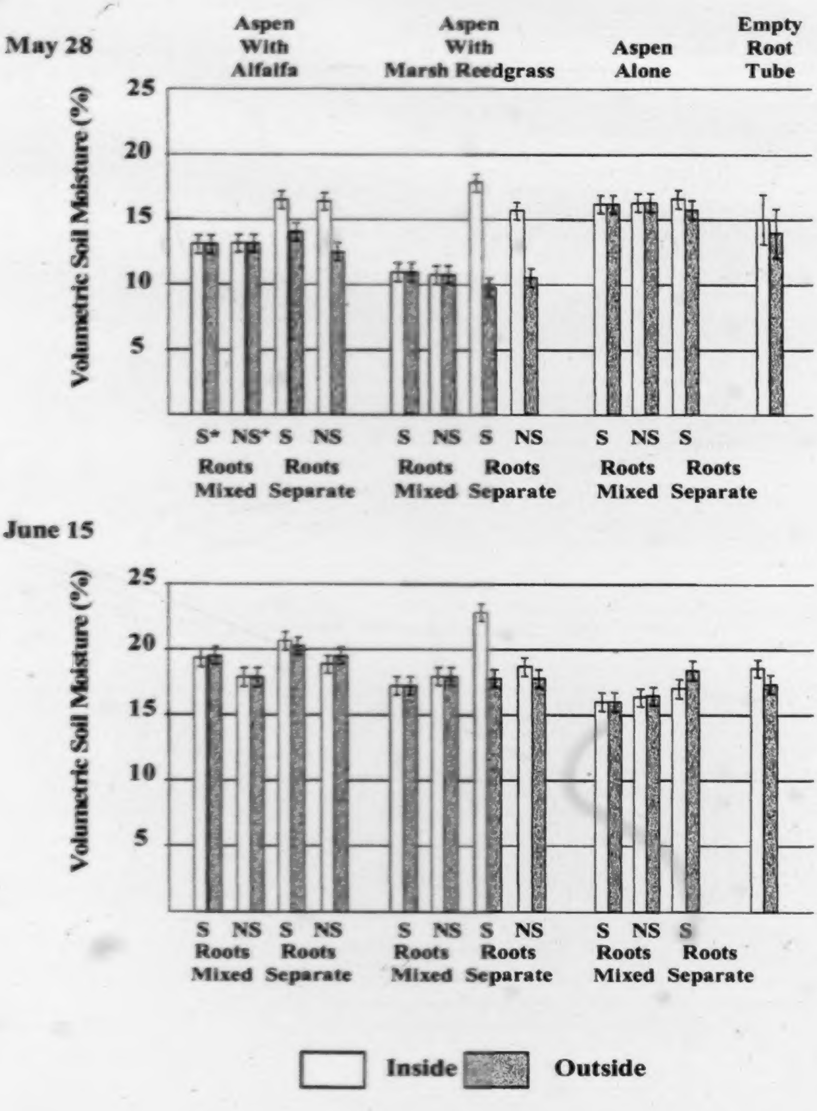


Figure 4-3 continued.

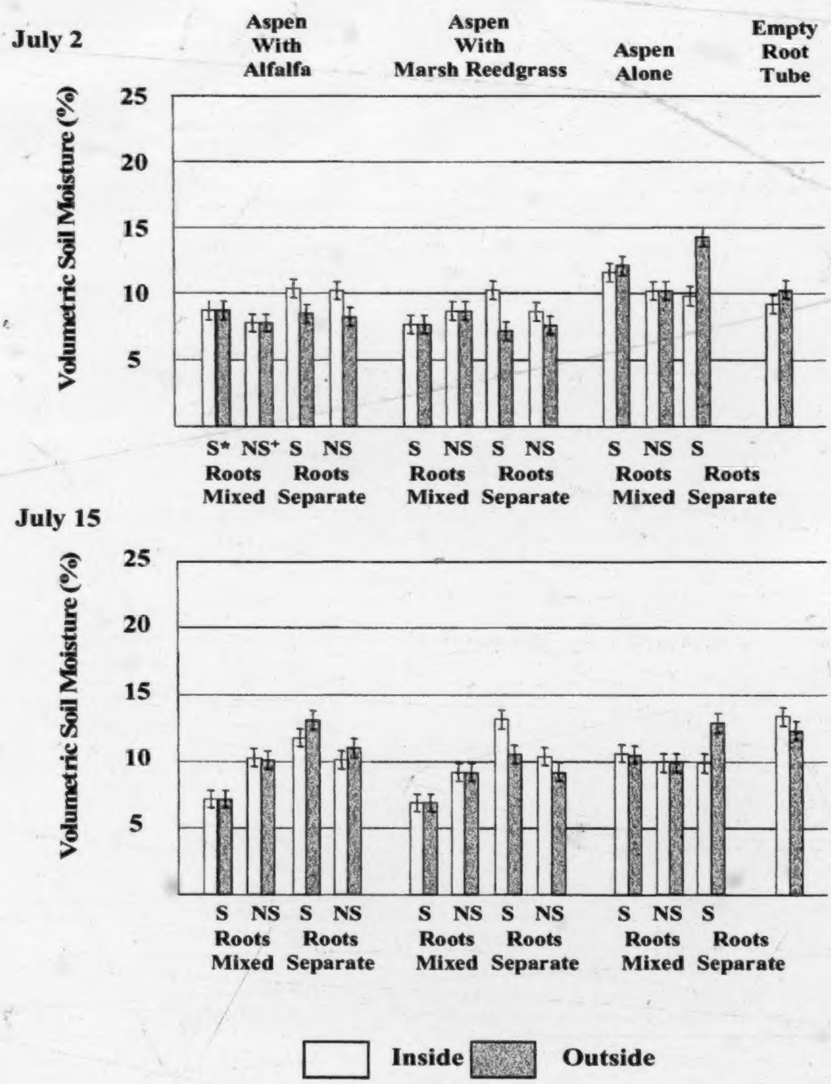
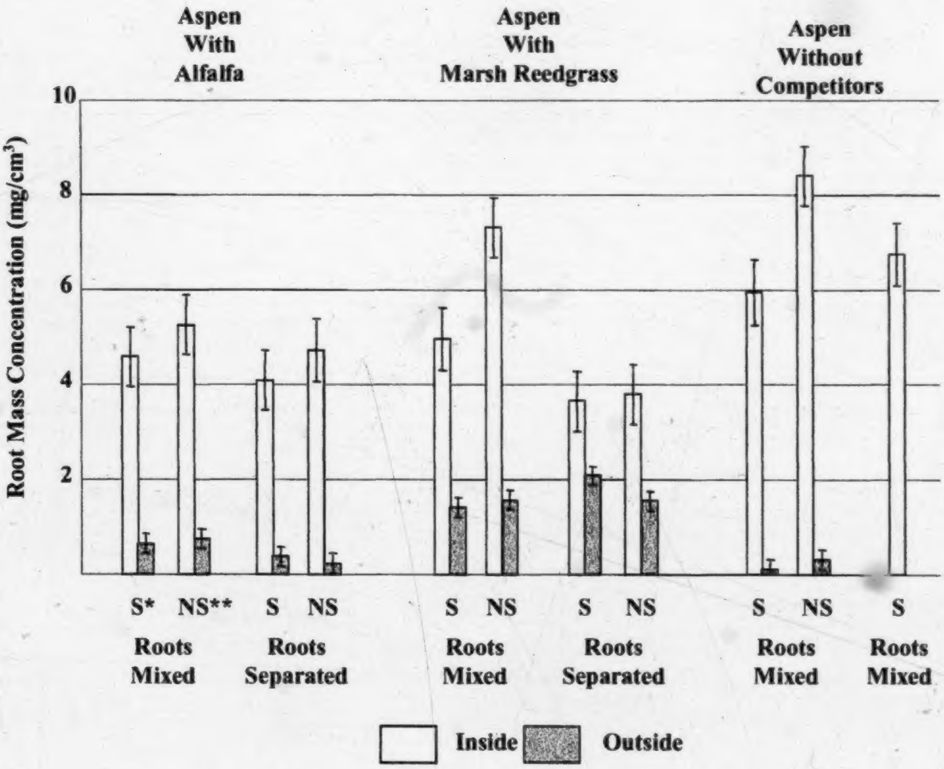


Figure 4-4 Root and shoot effects of alfalfa (*Medicago sativa* L.), marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) and aspen (*Populus tremuloides* Michx.) seedlings on root mass concentration in the upper 15-cm of soil, July 2002. "Inside" samples from within root exclusion tubes or corresponding distance from aspen on plots without below-ground barrier. "Outside" samples from interspace between aspen and surrounding vegetation, outside of root exclusion tubes or corresponding distance from aspen on plots without below-ground barrier. *Shoots of surrounding vegetation intermixed with aspen stem (S). **Shoots of surrounding vegetation separated from aspen stem (NS).



4.4 Literature Cited

Bailey, A.W., and R.K. Gupta. 1973. Grass – woody plant relationships. Canadian Journal of Plant Science 53: 671-676.

Callaway, R.M. and L.R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958-1965.

Cahill, J.F. Jr. 2002. Interactions between root and shoot competition vary among species. Oikos 99: 101-112.

Cannell, M.G.R. and J. Grace. 1993. Competition for light: detection, measurement and quantification. Canadian Journal of Forest Research 23: 1969-1979.

Coomes, D.A. and P.J. Grubb. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs 70(2): 171-207.

Daubenmire, R. 1959. A canopy coverage method of vegetational analysis. Northwest Science 33: 43-61.

He, Z.L., A.K. Alva, D.V. Calvert and D.J. Banks. 1999. Ammonia volatilization from different fertilizer sources and effects of temperature and soil pH. Soil Science 164: 750-758.

Hendershot, W.H., H. Lalande and M. Duquette. 1993. Ion exchange and exchangeable cations. Chapter 19, pp 167-175 *in*: Carter, M.R. (editor) Soil Sampling and Methods of Analysis. Canadian Society of Soil Science, Lewis Publisher, Boca Raton, FL, 823 p.

Hobbie, S.E. and F.S. Chapin III. 1998. An experimental test of limits to tree establishment in Arctic tundra. Journal of Ecology 86: 449-461.

Landhäusser, S.M. and V.J. Lieffers. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis canadensis*. Canadian Journal of Forest Research 28:396-401.

Liebig, J. von. 1840. Organic chemistry in its applications to agriculture and physiology microform. Edited from the manuscript by Lyon Playfair. Taylor and Walton, London.

Littell, R.C., W.W. Stroup and R.J. Freund. 2002. SAS® for Linear Models, Fourth Edition. SAS Institute Inc., Cary, NC, 466 p.

Maynard, D.G. and Y.P. Kalre. 1993. Nitrate and exchangeable ammonium nitrogen. Chapter 4, pp 25-38 *in*: Carter, M.R. (editor) Soil Sampling and Methods of Analysis. Canadian Society of Soil Science, Lewis Publisher, Boca Raton, FL, 823 p.

Montieth, J.L. 1977. Climate and efficiency of crop production in Britain. Philosophical Transactions of the Royal Society of London B 281: 277-294.

Perala, D.A. and D.H. Alban. 1982. Biomass, nutrient distribution and litterfall in *Populus*, *Pinus* and *Picea* stands on two different soils in Minnesota. Plant and Soil 64: 177-192.

Pregitzer, K.S. and A.L. Friend. 1996. The structure and function of *Populus* root systems. Chapter 14 *in*: Stettler, R.F, H.D. Bradshaw, P.E. Heilman, and T.M. Hinkley (editors). The Biology of Populus and its Implications for Management and Conservation. National Research Council Research Press, Ottawa, Ontario, pp 331-354.

Rivard, P.G., P.M. Woodward and R.L. Rothwell. 1990. The effect of water table depth on white spruce (*Picea glauca*) seedling growth in association with the marsh reed grass (*Calamagrostis canadensis*) on wet mineral soil. Canadian Journal of Forest Research 20: 1553-1558.

Ruark, G.A. 1990. Evidence for the reserve shelterwood system for managing quaking aspen. Northern Journal of Applied Forestry 7: 58-62.

Strong, W.L. and K.R. Leggat. 1992. Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife, Edmonton, AB, 59 p.

Walton, P.D. 1983. Production and Management of Cultivated Forages. Reston Publishing Company, Inc., Reston, Virginia. p 240.

Welden, C.W. and W.L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Quarterly Review of Biology 61: 23-44.

Wilson, J.B. 1988. Shoot competition and root competition. Journal of Applied Ecology 25: 279-296.

CHAPTER 5

Effects of Aspen Canopy Removal and Root Trenching On Understory Microenvironment and Soil Resources

5.1 Introduction

Ecological processes affecting plant growth in agroforests are closely linked to microclimatic conditions. In forest environments, resource levels are stratified and their availability in the understory depends on both the absolute amount present and the proportion available after use or modification by the overstory (Kho 2000). Free-growing aspen (*Populus tremuloides* Michx.) by definition have extended their canopy above the shading influence of the herb and shrub layers and can have important influences on the energy balance, water relations and soil nutrients in the understory (Brenner 1996). These changes in the microclimate and resource availability produce an array of effects for understory plant growth.

Trees block insolation and airflow to their understory. This simultaneously reduces photosynthetically active radiation (PAR) and air temperature (T), and increases relative humidity (RH) in the understory (Jones 1992). PAR reductions below the optimum for photosynthesis are detrimental to understory production. Conversely, decreased T and wind and increased RH can reduce leaf-to-atmosphere vapour pressure differences (D) and thereby promote photosynthesis (Dang *et al.* 1997). Under warm, dry atmospheric conditions, combinations of high leaf T and low atmospheric humidity result in a large D. This creates a strong gradient for the movement of water from plant to atmosphere and unchecked would result in desiccation or xylem cavitation. As a survival mechanism, a large D initiates leaf stomate closure to conserve water by slowing or stopping transpiration. However, this simultaneously restricts or temporarily suspends photosynthetic gas exchange in plants utilizing the 'C3' photosynthetic pathway (Dang *et al.* 1997) and to a lesser extent in 'C4' plants. Potential facilitation of understory growth through D reductions is more likely expressed in hot, dry biomes, however this process has also been observed in subalpine systems (Young and Smith 1982, Young and Smith 1983). Similarly, Marsden *et al.* (1996) found enhanced stomatal conductance and net assimilation in white spruce (*Picea glauca* (Moench)

Voss) with T and humidity modifications that could result from boreal aspen canopies. Likewise, beaked hazelnut (*Corylus cornuta* Marsh.) daytime stomatal conductance was inversely related to D (r^2=0.45) when D>0.5 kPa (Hogg *et al.* 2000). On sunny days with a high ambient D there were significant declines in photosynthesis even with adequate soil moisture, although the authors concluded differences in daily assimilation rates appeared to be influenced more by solar input than D.

Low T can also suppress understory plant growth and is an important factor for production in northern ecosystems. The boreal region is restrictive for plant growth because of both a short growing season and cold, nutrient-poor soils (Bonan and Shugart 1989). The length of the growing season is dictated by first and last killing frosts each year, and less severe events can reduce photosynthetic capacity and thereby restrict annual growth. Trees can have a moderating influence on the radiative balance in cold climates through the emission of long-wave radiation. Although not photosynthetic, long-wave radiation reduces the incidence of radiative frosts and thereby extends the growing season in the understory by reducing or eliminating frost damage. For example, while white spruce seedlings in the open and under aspen had similar photosynthetic rates in summer, photosynthesis decreased in the open during the spring and fall attributed to increased frost (Man and Lieffers 1997). Likewise, late-spring radiative frosts were reduced by a mixed boreal overstory in comparison to clear-cut areas, resulting in earlier spruce seedling bud-break (Groot and Carlson 1996). Moreover, although the northern growing season is relatively brief, surface T can reach levels that damage plant tissue and thereby reduce total annual production. Tree canopies can also buffer understory plants from these summer T extremes.

Trees can affect the understory soil moisture balance both positively and negatively. An overstory layer can enhance soil moisture by reducing evaporation resulting from blocking solar input and airflow (Smith 2000). Reduced evaporation under tree canopies is common where potential evapotranspiration exceeds precipitation in the open. However, net increases in soil moisture are not expected in environments with inherently low evaporation or extremely high precipitation, such that soils are generally near field capacity the majority of the time (Coombs and Grubb 2000).

Moreover, these soil water gains must be balanced against water diversion and uptake by trees. Canopies reduce moisture reaching the understory by intercepting precipitation and channelling it towards the tree bole; in fact, small precipitation events may be entirely intercepted (Anderson *et al.* 1969). Trees also draw on soil moisture with potential overlap of use with understory herb and shrub vegetation. Indeed, the majority of aspen roots are concentrated in the upper 20 cm of boreal soils, and there is a negative correlation between herb cover and aspen root density (Strong and La Roi 1983).

Soil nutrient levels are also potentially affected by a forest overstory through changes to soil T and soil moisture, and nutrient inputs from leaf litter. In addition to these modifications, nutrient uptake and immobilization in tree biomass must also be factored into the overall impact of a forest overstory. In warmer climates, lower subcanopy soil T can facilitate greater microbial growth and increase soil nitrogen (N) mineralization (Wilson 1990). However, mineralization is more likely to be impeded by low soil T in northern climates and reduced insolation by trees may therefore negatively impact soil N availability. Likewise, litter accumulation can enhance or hinder understory development depending on its volume and chemical properties. Small amounts of tree litter may reduce evaporation from the soil and release nutrients as it breaks down (Smith 2000). Conversely, large amounts of tree leaf litter can 'smother' and greatly reduce or eliminate understory vegetation. Thick surface litter layers can also prevent soil warming which can restrict soil warming in the spring and compound the negative effects of cold soils on plant growth.

Agroforestry systems are designed to optimize the biological returns from mixtures of trees and herbaceous crops. The development of sustainable management prescriptions, in turn, requires an understanding of the influence of microclimatic and soil parameters on plant growth. Given the potential complex array of simultaneous conflicting positive and negative overstory effects, new information is needed to identify the influence of aspen stands on the physical environmental conditions in their understory. This information can then be used to develop agroforestry systems that strategically minimize competitive and maximize facilitative effects.

5.2 Objectives and Null Hypotheses Tested

This experiment selectively manipulated aspen canopy and rooting zone influences to determine the individual and collective influences on the understory microenvironment and soil resource levels. Specific objectives were to determine the effects of aspen stem removal and root trenching on understory PAR, air T, RH, soil moisture and available soil N. The following null hypotheses were tested:

1. aspen canopy removal has no effect on subcanopy PAR levels, air T, RH, soil moisture or available soil N;
2. root trenching under aspen has no effect on soil moisture or available soil N; and,
3. the interaction of aspen canopy removal and root trenching has no effect on subcanopy PAR levels, air T, RH, soil moisture or available soil N.

5.3 Methods

Research Sites

Research was conducted at two sites in central Alberta containing juvenile (15-20 year old) aspen stands. The first site ('Boreal') was located in the Lower Boreal Mixedwood natural region (Strong and Leggat 1992) southwest of Lac La Biche, Alberta (54° 33' N, 112° 05' W) on the Lakeland Agricultural Research Association lease. The Boreal site receives 504 mm of precipitation annually with approximately half during the growing season (1970-2000 normal, Environment Canada). Aspen at the Boreal site at the beginning of the experiment were 18-20 years old, at an average density of 16,319 ± 367 stems ha^{-1}, height of 5.7 ± 0.2 m, and basal area of 22.7 ± 1.7 m^2 ha^{-1}. Native shrubs and forbs including low-bush cranberry (*Viburnum edule* (Michx.) Raf.), prickly rose (*Rosa acicularis* Lindl.) and wild sarsaparilla (*Aralia nudicaulis* L.) dominated the understory vegetation at the beginning of the experiment.

The second site ('Parkland') was located in the Aspen Parkland natural region, north of Kinsella, Alberta (53° 00' N, 111° 32' W) on the University of Alberta's Research Ranch. The Parkland site was situated on well-drained, glaciolacustrine sediments and receives 431 mm of precipitation annually with more than 70% during the April to September growing season (1970-2000 normal, Environment Canada). Aspen at the Parkland site at the beginning of the experiment were 15-18 years old, at an average density of 13,194 ± 1,696 stems ha^{-1}, height of 6.3 ± 0.2 m, and basal area of 25.4 ± 1.7 m^2 ha^{-1}. Understory vegetation was dominated by native shrubs, principally western snowberry (*Symphoricarpos occidentalis* Hook.) and prickly rose, and a mixture of native and introduced grasses, including smooth bromegrass (*Bromus inermis* Leys).

Treatments and Experimental Design

Nine, 10- x 10- m macroplots were selected at each site for relative uniformity of aspen density and size, topography, slope and aspect to minimize the potential confounding effects of these variables. Treatments were applied in a split-plot design. Three levels of aspen canopy removal were randomly applied three times each to macroplots (main plots) by cutting the appropriate number of aspen stems off at ground level. The following canopy removal treatments were tested:

1. no aspen canopy removal (control);
2. partial canopy removal (equal to the amount necessary to increase insolation by approximately 100%); and,
3. full aspen canopy removal.

Partial canopy removal was conducted such that remaining stems were approximately equidistantly spaced and evenly distributed across the macroplots, with an average post-thinning density of 6,770 ± 640 stems ha^{-1}. Aspen stems cut for the canopy removal treatments were removed from the macroplots. Macroplots were set a minimum of 5-m apart, as well as a minimum of 5-m from major openings or atypical site conditions to minimize edge effects around the treatment units. Resprouting (suckering) aspen originating from the roots or stem base of treated areas were removed biweekly during the aspen growing seasons.

Within each macroplot, three root trenching treatments were applied on 0.5- x 2.0-m (1 m^2 area) rectangular subplots in the centre of the aspen canopy removal macroplots (Figure 5-1). The following treatments were applied to the subplots:

1. trenched with a root barrier;
2. trenched and no barrier control; and,

3. untrenched control.

Each root trenching treatment was replicated twice in each macroplot, for a total of six subplots per macroplot. To minimize potential edge effects from the macroplots on the root trenching treatments, a 3-m buffer was established between the outside edge of the subplots and perimeter of the macroplots. Subplots were randomly assigned to one of eight positions within the centre of the macroplots inside the inner bound of the buffer, with 50-cm buffers between subplots (Figure 5-1). Subplots requiring trenching were trenched 5-cm wide to a depth of 40-cm. This depth is below the main surface roots of aspen and accompanying understory vegetation (Strong and La Roi 1983). The 'trenched with barrier' plots were lined with two layers of 6-mil (150 μm) clear plastic sheeting to prevent regrowth of aspen roots into the subplots.

Measures

Direct measures of PAR (μmol m^{-2} s^{-1} of radiation in the 400 to 700 nm bands) were made with quantum sensors. In 2000 and 2001, measures were taken with a Decagon AccuPAR™ ceptometer; in 2002, a LICOR, LI-190SA™ quantum sensor was used. At each sampling date, 10 instantaneous PAR measurements were taken at four random locations in each subplot and averaged. Measurements were conducted over a 3-hr period centred around solar noon under uniform conditions of cloudless skies, corresponding to the approximate maximum annual leaf area of the aspen. Fractional PAR interception by the overstory was calculated for each subplot by comparing the understory measures to readings in openings with an unobstructed sky view, taken within 30 to 60 s of each other.

Understory boundary-layer air T (to the nearest 0.1°C) and RH (to the nearest 0.1%) were measured 50-cm above ground level in each macroplot. In 2000 and 2001, measures were taken with an Oakton™ digital thermohygrometer coincident with PAR measurements over each subplot and averaged for each macroplot. In 2002, T, RH and absolute humidity (AH, to the nearest 0.1 g m^{-3}) were recorded at 5-minute intervals with data loggers (Onset Computer Corporation, HOBO H8 Pro RH/Temp™) located in the centre of each canopy removal macroplot from late April until mid-October.

Daily precipitation and air T were obtained from Environment Canada weather stations located in the local area of each research site. Data and 30-yr normals for the Parkland site were obtained from the Kinsella Research Ranch weather station located approximately 4 km south of the research plots. Data for the Boreal site were compiled from three different weather stations within a 25-km radius of the research site. A primary data set was obtained from the Venice station (54° 40' N, 112° 04' W) with additional data from two weather stations in the vicinity of the municipality of Lac La Biche (both at 54° 46' N, 112° 01' W). Long-term weather normals for this area were only available from a fourth site (Athabasca, 54° 49' N, 113° 32' W).

Gravimetric soil water samples from the upper 10-cm of mineral soil were collected from each subplot at peak aspen leaf area in early August 2001. Volumetric soil moisture in the upper 10-cm of mineral soil (to the nearest 0.1%) was recorded in each subplot at 3-week intervals from May until October 2002 with a Delta-T™ theta probe. Four theta probe measures were conducted on each subplot at each sampling date in 2002, and averaged. When necessary, an area of surface litter just large enough to permit probe insertion was removed to ensure the theta probes only contacted mineral soil. Litter was replaced to its original position immediately following measures.

Four, 2- by 15-cm soil cores were extracted from each subplot at approximate peak herbaceous biomass in 2002, and again after snowmelt, but prior to initiation of aspen or understory growth, in April 2003. At each sampling, the four cores from each subplot were combined. Core locations for the first sampling period were determined randomly. Sample locations were assigned to a new position within the subplot during the second sampling with a restricted randomization such that they did not occur on the same areas from which previous samples had been removed. Soil samples were screened from the air-dried cores through a 2-mm Canadian Standard Sieve. Available nitrate (NO_3-N) and ammonium (NH_4-N) was determined by spectral absorption after extraction from the soil with a 5:1 mixture with 2 *M* KCl (Maynard and Kalre 1993).

Analyses

Temperature and humidity were analyzed with a multi-staged approach. Hourly averages were calculated for data logged in 2002 for each canopy treatment at each site and were plotted across all sampling dates (27 April to 12 Oct) to identify patterns. Both RH and T typically followed repeating diurnal patterns (see sample data, Figure 5-2), but AH did not. Although the magnitude and range of fluctuation varied with weather patterns, T increased predictably with solar input to a mid-day high and then decreased sharply coincident with the setting sun. Temperatures dropped to a minimum overnight as a result of radiative losses, and then reversed to begin the cycle again with the new sunrise. In an inverse, complementary pattern, RH decreased daily to a mid-afternoon low with warming of the air and then gradually increased with air cooling through the remainder of the day. Differences between the canopy treatments, when evident, occurred during peak heating or cooling for the day (also corresponding to minimum and maximum RH). As a result, parametric analyses of the effects of aspen canopies were conducted on subsets of the T and RH data corresponding to these periods. Repeated measures analyses of variance (RMANOVA) using general linear models[1] (Littell *et al.* 2002) were conducted on average mid-day T (11:00 to 15:00), AH and RH (13:00 to 15:00), as well as on the daily maximums and minimums. Coefficients output from the RMANOVA appeared to display unstructured covariance between days. When significant effects existed across all days ($p<0.001$), differences due to aspen canopy treatments on individual days were determined by univariate analysis of variance (ANOVA) using mixed linear models (Table A2-9, Appendix 2). Bonferonni corrections were applied to the ANOVAs to reduce the probability of type I errors.

The proportions of PAR, RH and T in each canopy treatment relative to conditions in proximate large openings were calculated at peak aspen leaf area in each year (early August). Instantaneous, concurrent measures of PAR, RH and T were made in 2000 and 2001; PAR data collected in 2002 was matched to the corresponding closest records from the onsite data loggers. Annual differences in these repeated measures were analyzed with mixed linear models (Table A2-10, Appendix 2, Littell *et al.* 2002). Likewise, treatment effects of canopy removal and root trenching on soil parameters were assessed using a repeated measures analysis of variance for a split-plot design, using mixed models (Table A2-11 and A2-12, Appendix 2).

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[1] RMANOVA using general linear models assumes unstructured covariance between sampling periods. Analysis with mixed models permit explicit examination of the covariance structure, unfortunately this data set (169 sampling dates) was too large for the available computational resources.

Data were checked for normality and homogeneity of variance and were found to meet these assumptions for parametric analyses. Kenward-Roger corrections were applied to the error degrees of freedom in the mixed model analyses to overcome any bias resulting from small sample size. Differences between specific canopy and root trenching treatments were determined with individual degree of freedom contrasts. Sites, canopy removal and root trenching treatments were assumed to have fixed effects; variation between treatments (assessed with replication) was assumed to introduce random effects. The covariance models used in the mixed repeated measures analyses were selected iteratively for each response variable by testing several structures and comparing Schwarz's Bayesian information criterion. This test is based on the maximum likelihood fit corrected for the number of parameters in the model, analogous to the adjusted R^2 employed in multiple regression analyses. Covariance between sampling periods for PAR, RH and T, soil moisture and soil N all displayed compound symmetry.

5.4 Results and Discussion

Weather Patterns

The Parkland experienced a pattern of progressively drier growing seasons over the course of the experiment. Total annual precipitation at the Parkland site was 462, 224 and 234 mm in 2000, 2001 and 2002, respectively. These values equate to 7% above the 30-yr normal in 2000, but only 52 and 54% of normal in the latter two years. Precipitation was 32% above normal at the Boreal site in 2000 due primarily to 1-m of snowfall above the February normal. Precipitation at the Boreal site in 2001 and 2002 were 403 and 397 mm, respectively, both slightly less than 80% of normal. Conditions were particularly dry early in the 2002 growing season; only 11% of the normal precipitation was received from May to June in the Parkland and 23% of the 30-yr normal fell in the Boreal. Indeed, this was the most severe drought recorded for this period in both the Parkland and Lower Boreal areas of Alberta. Weather patterns were further distorted from normal in 2002 by high and low T extremes. An exceptionally cool spring delayed the start of the growing season with mean April T for both sites below freezing, in contrast to 4.2 to 4.6°C normals. This was followed by early-August frost at both sites, when normally there are no days with freezing T at either site. At the other extreme, the summer drought was compounded by above-normal July T, as evidenced by 7 d in July above 30°C at the Boreal site, well above the 30-yr normal of 0.2 d. The Parkland site recorded 12 d in July above 30°C, also well in excess of the normal of 1 d. This included 2 d that set all-time maximum T records.

Temperature

Air T in the understory vegetation boundary layer is a result of a complex and dynamic balance of solar input and radiative losses and gains. The overstory canopy layer is the controlling factor in radiative exchanges in forested ecosystems (Oke 1993). Solar radiation is usually the primary source of energy input to the surface air layers and can be augmented or diminished by air movement into and out of the microsite, as well as through long-wave radiation emissions. Trees affect the energy balance directly by three mechanisms: by reflecting and absorbing solar input, by slowing and dissipating air movement, and by intercepting and emitting long-wave radiation.

Average daily minimum ($p=0.07$), maximum and mid-day T were greater ($p<0.0001$) at the Parkland site than the Boreal site. Because aspen canopies can influence all aspects affecting the dynamic balance in air T, not surprisingly, daily and overall seasonal differences in T were observed in relation to the canopy treatments. In general, aspen canopies had a moderating effect on air T, reducing maximums ($p<0.0001$) and increasing minimums ($p<0.0001$) relative to the openings. The diurnal fluctuations observed in T (Figure 5-2) showed season-long differences ($p<0.01$) in the average mid-day T. Mid-day T was lower (adjusted $p<0.05$) with either a partial or full aspen canopy than in the openings (Figure 5-3). Moreover, aspen buffered average daily maximum T ($p<0.0001$). Daily maximum T was lower (adjusted $p<0.05$) with a partial or full canopy than in the open on most days of the 2002 growing season at both sites (Figure 5-4).

Furthermore, lower maximum T under full aspen canopies in relation to partial canopies occurred on 23 d in 2002, usually coincident with mid-day average T > 25°C from mid-June through to the end of July (Figure 5-4). In comparison, Carlson and Groot (1997) found very little variation in average T (0.7°C) between closed aspen stands and aspen clear-cuts; however, they also noted greater T extremes in the aspen clear-cut.

Temperature moderation by aspen at both sites had added importance in preventing extreme maximum T. Without an aspen canopy, the maximum T in the understory boundary layer at the Parkland site exceeded 40°C on 8 d in 2002, whereas this T threshold was only exceeded on 3 and 2 d under partial and full canopies, respectively (Figure 5-4). Similarly, maximum T exceeded 40°C on 2 d at the Boreal site without aspen cover, but did not reach this T maximum with either a partial or full aspen canopy. Grace (1983) suggests the lethal T for many terrestrial plants is around 50°C. Temperatures above 40°C, while not lethal, are damaging to photosynthetic processes and protein denaturation can occur in plant tissues. Additionally, elevated leaf T resulting from the higher air T, coupled with lower RH, increases D (see Chapter 8, this volume), which can restrict understory plant growth by slowing or stopping photosynthetic gas exchange.

Aspen also moderated daily minimum T. In addition to season-long effects of increasing minimum T ($p<0.001$), aspen cover prevented frosts. In general, long-wave radiation losses from the understory are intercepted by the overstory and re-emitted to the ground layer (Oke 1993). This can prevent net heat loss to open skies and eliminate the occurrence of radiative frosts. This phenomenon was observed at both sites over the 2002 growing season. At the Parkland site, the last date on which all plots experienced understory air T below 0°C was 26 May (Figure 5-5). From 27 May until 14 September the daily minimum T under full aspen canopy did not fall below 0°C. In contrast, frosts occurred later in the spring under a partial aspen canopy at the Parkland site on 27 May and 1 June. Moreover, without aspen cover, radiative frosts were recorded on five dates (27 May, 1 June, 4 August, 8 September and 13 September) during the frost-free period of full aspen canopy plots (Figure 5-5). These differences translate into frost-free periods at the Parkland site of 110, 104 and 63 d, for full, partial and no aspen canopy treatments, respectively. At the Boreal site the frost-free period for both the partial and full aspen canopy treatments extended for 105 d from 8 June to 22 September (Figure 5-5). In contrast, with complete aspen removal radiative frosts were recorded on six dates (19 June, 3 July, 4 August, 17 August, 14 September and 18 September) during this period, providing for a relatively brief 31 d frost-free period (Figure 5-5). While none of the growing season radiative frosts were severe enough or of sufficient duration to kill understory vegetation, frosts have been demonstrated to reduce photosynthesis (Man and Lieffers 1997), and thus likely reduced understory production without aspen cover.

Differences in relative proportions of subcanopy RH and T at peak aspen leaf area both showed strong ($p<0.0001$) annual variation, due primarily to the changes associated with canopy removal (Figure 5-6). The proportion of RH relative to open conditions was similar ($p=0.72$) at both sites, whereas T reductions due to aspen canopy were more acute ($p=0.06$) at the Boreal site. Effects of the aspen canopy treatments across years were marginal for RH ($p=0.09$), but more substantial for T ($p<0.001$). Moreover, for both variables there were strong annual differences ($p<0.01$) in the effects of canopy removal. Pre-treatment RH ($p=0.61$) and T ($p=0.67$) proportions did not differ, nor did they in the year following (2001) stem removal ($p>0.10$, Figure 5-6). However, there were strong effects of the overstory on both RH ($p=0.02$) and T ($p<0.0001$) proportions in 2002. The proportion of large opening RH was lower with complete canopy removal than either under a partial ($p=0.07$) or full canopy ($p=0.04$). However, these ratios did not differ ($p=0.77$) between the two aspen canopies. The same pattern was observed for T proportions, although they had negative effects on T profiles. The relative proportion of T was greater with complete canopy removal than either under a partial ($p=0.01$) or full canopy ($p<0.001$) in 2002, whereas T proportions did not differ ($p=0.11$) between the full and partial canopy treatments. There is no apparent ecological explanation for the lack of aspen effects on RH and T proportions in 2001. Post-hoc analysis of interannual microclimate variability revealed low power to detect differences between canopy treatments for both RH ($1-\beta = 0.38$) and T ($1-\beta = 0.54$). This underscores the importance of longer-term or more frequent measures to adequately characterize highly dynamic environmental variables.

Humidity

In general, microsite humidity is dictated by air T and weather patterns. Absolute humidity levels are governed by evapotranspiration rates and movement of moisture-laden air masses vertically and horizontally with the predominant weather patterns (Oke 1993). Throughout 2002 there were greater AH levels ($p<0.0001$) at the Boreal site than the Parkland site. At both sites, aspen influenced the maximum daily AH ($p<0.001$), but not the daily minimum AH ($p=0.94$). When daily differences were noted, maximum AH was greater (adjusted $p<0.05$) with complete canopy removal than either partial or full aspen canopies (Figure 5-7). Differences between the canopy treatments on individual days were sporadic until mid-July, and then more regular, coincident with greater rainfall in the latter half of the growing season. Greater evaporation from the soil, coupled with increased transpiration from the greater amount of understory vegetation with complete canopy removal (see Chapter 6, this volume) are possible mechanisms for the AH differences. Moreover, these differences likely didn't manifest as frequently during the early-season drought because soils had become equally dry, regardless of the amount of overstory.

Relative humidity is governed by AH and air T, and therefore seasonal RH reflected the patterns of these other environmental variables. In addition to diurnal differences observed across sites and canopy treatments (Figure 5-2), minimum and maximum daily RH were greater ($p<0.0001$) at the Boreal site than the Parkland site throughout 2002, reflecting both cooler T and higher AH in the Boreal. Although minimum RH did not differ ($p=0.38$) between the aspen canopy treatments, maximum daily RH did ($p<0.001$) vary with aspen cover. Greater night time cooling in the openings (decreasing the water holding capacity of air), coupled with greater AH in the same, resulted in higher RH in the openings at night than with either full or partial canopy cover. Moreover, although over the entire 2002 growing season mid-day RH did not differ ($p=0.19$) between canopy treatments, it did relate significantly to aspen canopy cover when examined in relation to precipitation patterns. During the drought period from late April to 15 July, RH was greater ($p<0.01$) with partial or full aspen canopies (Figure 5-8). With the onset of more normal precipitation patterns at both sites from 16

July onward, average mid-day RH did not differ (p=0.38) between canopy treatments. Differences in RH dynamics therefore tended to only be expressed at the extremes (diurnal or seasonal) of other microclimatic conditions (e.g. T or precipitation).

Photosynthetically Active Radiation

As expected, aspen canopy cover reduced PAR reaching the understory at peak annual aspen leaf area over all years of the study (p<0.0001), with consistent differences between all levels of aspen canopy (p=0.001 to <0.0001, Figure 5-9) post-treatment. However, there were also differences (p=0.02) in the relative amount of PAR reaching the understory between sites. With complete canopy removal, 91 to 95% of the full open-sky PAR at solar noon was received at the Parkland site, whereas only 72% of open-sky PAR was received in the Boreal site openings in 2002 (Figure 5-9). Site differences between the complete canopy removal plots likely resulted from a combination of an increase in 2001-2002 tall shrub cover at the Boreal site (see Chapter 6, this volume) which intercepted some incident PAR, coupled with a lower solar angle and slightly greater aspen density, both of which blocked more lateral light penetration from the plots. In addition, although similar (p>0.10) between sites in 2000 and 2001, the proportion of open-sky PAR reaching the understory of the partial and full aspen canopy treatments at the Parkland site increased (p<0.0001) in 2002. In contrast, PAR under these canopy treatments remained similar to 2001 levels at the Boreal site (Figure 5-9).

The increase in subcanopy PAR at the Parkland site was coincident with aspen mortality during the drought (see Chapter 6, this volume). Increased subcanopy light at the Parkland site is consistent with the general patterns observed for PAR transmission in aspen stands noted in previous research. In general, aspen canopy density influences light transmission with an increase in understory PAR proportionate to reductions in leaf area, following Beer's Law (Cannell and Grace 1993). Aspen health and pest infestations influence leaf area, and hence light transmission. For example, drought and tent caterpillar defoliation can reduce Parkland aspen canopy cover by 20 to 90% of normal (Alexander 1995). Therefore surviving aspen at the Parkland site likely developed less leaf area during the 2002 drought. As a consequence, the proportion of open-sky PAR with a full aspen canopy at the Parkland site in 2002 (28 ± 4 %) equalled that of the partial canopy treatment (28 ± 4 %) at the Boreal site.

Soil Moisture

Soil moisture response was highly variable, changing through time with site, canopy and root effects, as well as the general precipitation patterns. Limited gravimetric sampling in 2001 showed both site differences ($p=0.04$) and a canopy effect ($p=0.04$) at peak aspen leaf area. Soil water was greater in the open (0.27 ± 0.02 g cm^{-3}) than under either a full (0.13 ± 0.02 g cm^{-3}) ($p<0.001$) or partial (0.15 ± 0.02 g cm^{-3}) ($p<0.01$) canopy at the Boreal site, but no differences appeared ($p>0.50$) with different canopy levels (0.16 to 0.18 ± 0.02 g cm^{-3}) at the Parkland site. Root trenching did not affect ($p=0.33$) soil water content at either site in August 2001.

More intensive soil moisture sampling in 2002 revealed overall strong site ($p<0.0001$) and canopy ($p<0.001$) effects, but marginal differences due to root trenching ($p=0.06$). Soil moisture levels differed between the Parkland and Boreal sites in three primary ways: absolute levels were greater ($p<0.0001$) at the Boreal site, the seasonal pattern of when significant treatment responses occurred through time differed ($p<0.0001$), as did the nature of the treatment effects. Shifting patterns of potentially competitive and facilitative conditions were related to the aspen overstory at the Parkland site, but generally neutral or potentially competitive effects occurred at the Boreal site.

Canopy or root effects were expressed ($p<0.05$) in all sampling periods at the Boreal site except during the peak of the drought, 11 July, when all soils had become uniformly dry (Figures 5-10, 5-11). In contrast, treatment effects were more transient at the Parkland site. Differences arose early ($p<0.0001$) in the 2002 growing season at the Parkland site, but as the drought intensified, all soils dried to the point that no differences ($p>0.50$) were observed between canopy or root trenching treatments from mid-June to mid-August. With late summer precipitation, canopy treatment differences ($p=0.03$) developed again at the Parkland site on 18 August, with the partial canopy displaying the greatest soil moisture. No significant ($p<0.10$) differences due to either aspen canopy or root effects were observed at the Parkland site over the remainder of 2002.

In addition to temporal differences in soil moisture between sites, the nature of treatment effects also varied. At the Parkland site, soil water was greater ($p<0.05$) with either a partial or full canopy than with complete canopy removal during the drought period from 13 May to 4 June (Figure 5-10). Soil moisture increased ($p=0.03$) again with partial aspen cover in mid-August. In contrast, during the first two sampling dates, soil moisture was greater ($p=0.01$ to 0.02) with complete canopy removal relative to a partial canopy at the Boreal site, but did not differ ($p>0.10$) from the full aspen canopy (Figure 5-10). As observed at the Parkland site, treatment differences disappeared at the height of the drought, but after soil moisture levels rebounded with August rainfall, levels were always greatest ($p<0.01$) with full canopy removal. Site differences in relation to aspen cover possibly reflect lower air T and greater shrub cover (see Chapter 6, this volume) at the Boreal site, both of which would have reduced evaporation from the complete canopy removal treatment. Reductions to total transpiration with aspen canopy removal may have also contributed to greater soil moisture content in the open. Soil moisture conservation with aspen cover at the Parkland site could have resulted from two mechanisms. First, aspen overstory blocked solar input, and hence reduced evaporation in the understory. Moreover, greater cover of aspen leaf litter was associated with increasing aspen cover (see Chapter 6, this volume). This additional litter would have further slowed evaporation and increased surface soil moisture.

When below-ground effects were expressed, they consistently indicated potential for competition for soil water through greater moisture availability in the trenched plots (Figures 5-11 and 5-12). Root trenching at the Boreal site increased soil water relative to the untrenched plots significantly ($p<0.05$) in sampling periods both before and after the severe soil drying at mid-summer and across all canopy treatments (Figure 5-11). A significant interaction of root trenching and canopy treatments ($p<0.05$) was recorded at the Parkland site. Root trenching with or without a barrier in place resulted in greater soil water ($p<0.05$) than the untrenched plots at the Parkland site from 13 May to 4 June, but only within the partial and full canopy plots. No difference ($p>0.50$) among trenching treatments occurred without aspen cover at the Parkland site (Figure 5-12). This may reflect an impact of canopy removal on root biomass in the complete canopy removal treatments. Removal of all the aspen stems on these plots would have restricted the photosyntate inputs to the aspen root system to those transferred via the underground clonal network from aspen in adjacent uncut areas. This could have resulted in a reduced below-ground competition on the untrenched controls within the complete canopy removal plots through fine root die-back. However, Shepperd and Smith (1993) found no declines in aspen roots (greater than 4-mm diameter) in the upper 20-cm of soil, 2 to 6 years following complete canopy removal in Montane aspen stands.

Increased soil water from the above-ground aspen effects at the Parkland site were masked in most periods when combined with below-ground effects on the same. However, a net increase in understory soil moisture availability (+5.2 %) was observed during the 4 June sampling (see comparison of highlighted values, Figure 5-12). Thus, greater water conservation than uptake by aspen buffered understory species from the full effects of the drought through that part of the growing season.

Soil Nitrogen

Soil N differences in relation to aspen canopy removal occurred at the Parkland site during the 2002 growing season, and again prior to initiation of plant growth in 2003 (Figure 5-13). Overall, NO_3-N and NH_4-N were lower ($p<0.0001$) at the Boreal site than the Parkland site, and no differences ($p=0.99$) were observed relative to aspen canopy cover at the Boreal site. Similarly, root trenching did not have an overall effect on soil N at either site, in either sampling period ($p=0.46$).

Soil N dynamics at the Parkland site reflect the conversion of NH_4-N to NO_3-N, and the influence of aspen cover. In 2002, NO_3-N did not differ ($p=0.82$) between canopy treatments at the Parkland site, but there were slightly higher levels ($p<0.01$) of NH_4-N within some canopy and root trenching combinations in comparison to complete aspen removal plots. During the following spring, the untapped soil-N pools had greater ($p=0.06$) average NO_3-N with a full canopy than in the openings, but there was no difference ($p=0.48$) between full and partial aspen canopies. Increased soil-N with a full aspen canopy could have resulted from aspen leaf litter inputs which also increased with corresponding increases in aspen cover (see Chapter 6, this volume). This may have been a primary source of NH_4-N in 2002, which was converted to the NO_3-N differences observed in 2003. However, canopy influences extended beyond direct litter inputs because the small differences in NH_4-N in 2002 between the canopy treatments separated into more substantial differences in NO_3-N levels in 2003. Conditions favouring mineralization under either full or partial aspen canopy, or greater volatilization or immobilization losses in the openings are possible explanations for this discrepancy. Thus, the moderating effects of aspen on T extremes may have positively influenced N mineralization.

Although root trenching did not produce significant overall results, a trend of greater soil-N in the untrenched plots was evident at the Parkland site (Figure 5-13). An inverse relationship between aspen competition (via full root interactions) and available soil N is counter-intuitive, unless examined with regards to understory biomass. Trenching, as previously noted, increased soil water, and this contributed to greater understory above-ground net primary production (ANPP). Soil N showed a negative relationship to ANPP (see Chapter 6, this volume). Thus, total N levels reflect the greater amount of understory vegetation in the trenched plots, giving the appearance of increased N availability when both aspen and understory species utilized the same soil area.

Conclusion and Management Implications

Results from 2002, which included record low precipitation and both abnormally high and low growing-season T, may seem anomalous to some. However, the 2002 growing season afforded a wide range of conditions to observe the effects of aspen stands on their understory microclimatic conditions and resource levels, particularly in examining infrequent threshold events (e.g. early August frost). Longer-term observations are needed and incorporation of over-winter measurements could also assist in the interpretation of data, particularly for soil moisture dynamics. For example, soil moisture conservation at the Parkland site during the drought seemed to incorporate a carryover of higher soil moisture levels from the over-winter period. Therefore, snow retention in relation to aspen cover needs to be investigated to quantify the relationship of aspen cover to soil moisture levels at the beginning of the growing season.

In general, the surface mineral soil layer is highly dynamic for soil moisture and N. This develops from the relative shallow rooting patterns of most species in these ecosystems and reduced buffering of environmental effects, including diurnal and seasonal T fluctuations and precipitation events, relative to deeper soil layers. The dominant variable governing soil moisture in 2002 appeared to be precipitation. Results of this experiment agree with those of Jose *et al.* (2000) who found that temporal soil moisture fluctuations in the 0-30 cm layer were greater than deeper soil profiles and closely followed the local precipitation patterns. However, further characterization of soil moisture and N in deeper profiles is needed to fully understand the dynamics and potential separation of resource use in northern agroforestry configurations.

The microclimatic results support the general theories on the importance of facilitation (Bertness and Callaway 1994, Brooker and Callaghan 1998, Holmgren *et al.* 1997). These theories postulate that net facilitation only becomes a significant ecological factor when buffering extremes in environmental conditions or disturbance. In both the Parkland and Boreal sites during periods of either above-average T or below average precipitation, aspen reduced the severity and extent of potentially adverse growing conditions. Moreover, aspen cover prevented growing-season radiative frosts, making the overstory the strongest factor in determining the length of the frost-free period. Conversely, while aspen consistently created a more humid environment during the drier part of the 2002 growing season, these changes are of questionable net benefit to understory growth. During the period of more normal rainfall and T regimes, modifications to RH are masked or insignificant in light of marginal differences in subcanopy air T and overall higher AH levels. Moreover, aspen canopies had less effect on day-to-day average T, which typically set growth rates through their influence on respiration and photosynthetic rates, than in moderating extreme high or low T. Thus, while the overstory plays a very important role relative to mitigating intermittent threshold events, with the exception of PAR reductions, it appears to have less consequence for growing conditions over longer periods of more normal, stable climatic conditions.

These results also provide direction for agroforestry design suitable for northern ecosystems. With the exception of PAR, there were very few season-long microclimatic differences between partial and full aspen canopies. Reducing aspen density doubled the amount of PAR reaching the understory (with associated increases in photosynthetic potential), but still retained many of the potentially facilitative microclimatic characteristics (moderation of T extremes, increased RH, and soil moisture conservation) of a closed forest. Balancing facilitative and competitive effects for the design of agroforestry system is therefore possible through further elucidation of the appropriate level of aspen cover. With a partial canopy, understory production gains proportional to increased PAR availability do not come with the full negative consequences of an open microclimate.

Figure 5-1 Layout of experimental plots used to test the effects of aspen (*Populus tremuloides* Michx.) canopy removal and root trenching.

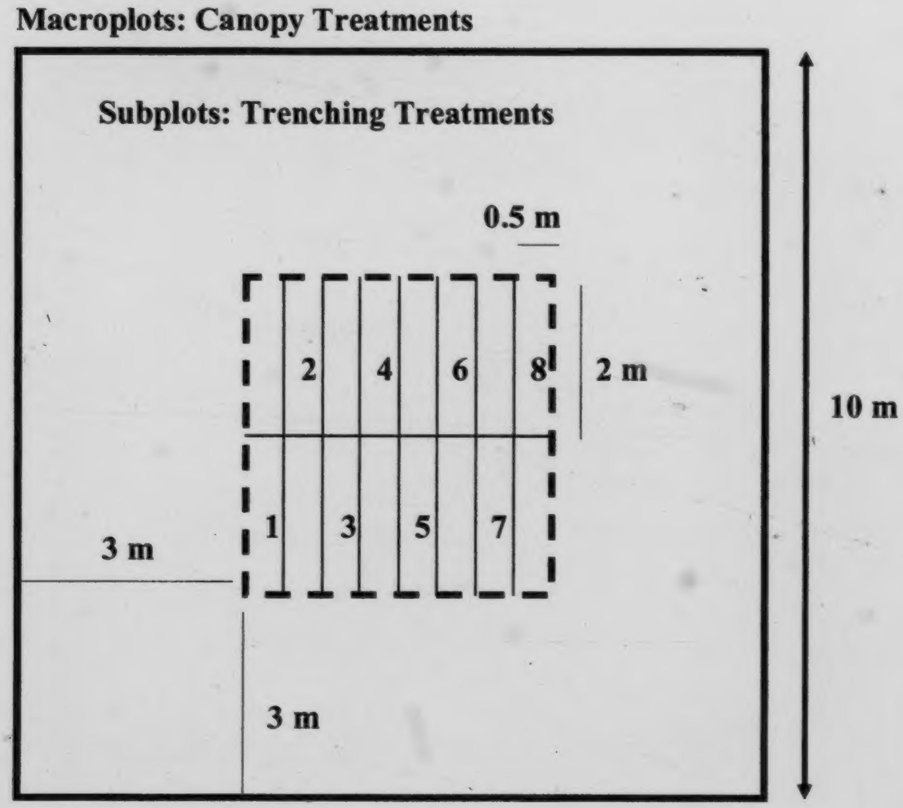


Figure 5-2 Effects of aspen (*Populus tremuloides* Michx.) canopy on typical diurnal patterns of understory air temperature and relative humidity 50-cm above ground at the Parkland site, from 7 to 13 June, 2002.

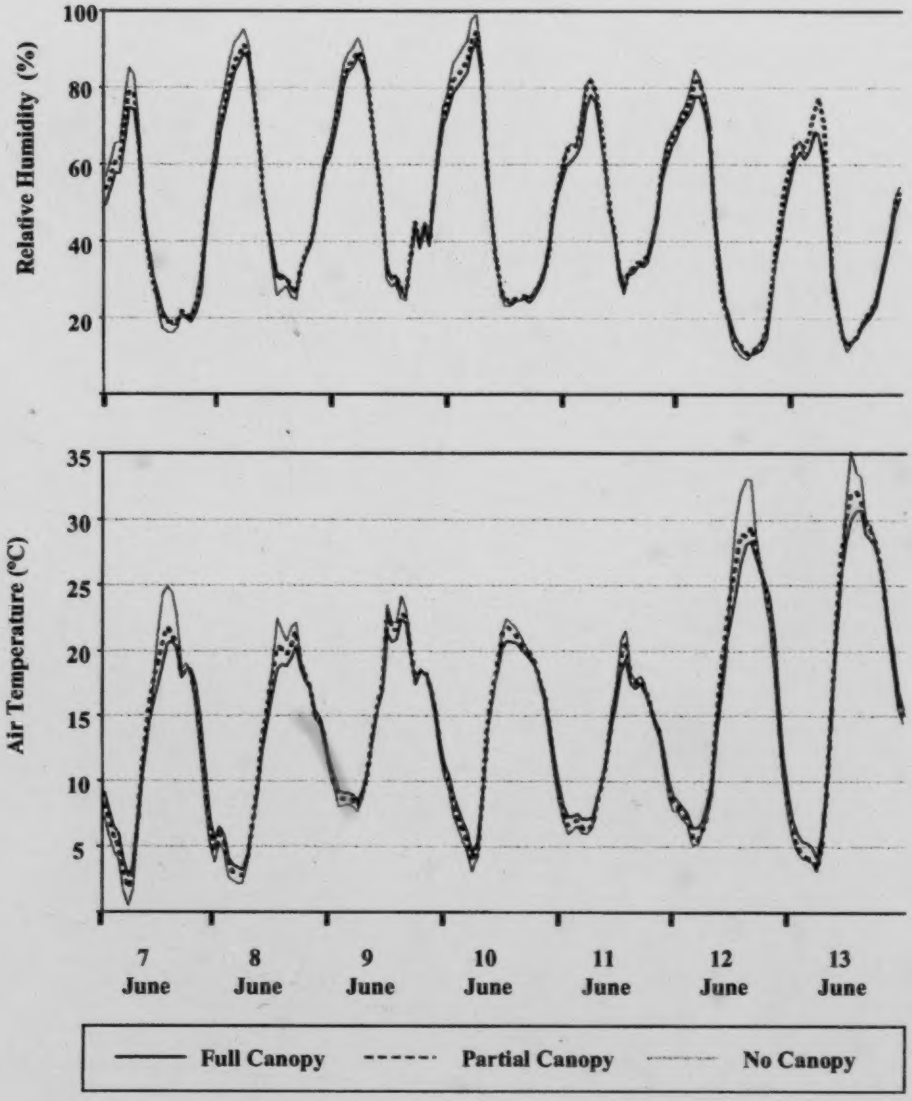


Figure 5-3 Effects of aspen (*Populus tremuloides* Michx.) canopy on average midday (11:00 to 15:00) temperature 50-cm above ground between 27 April and 11 October, 2002.

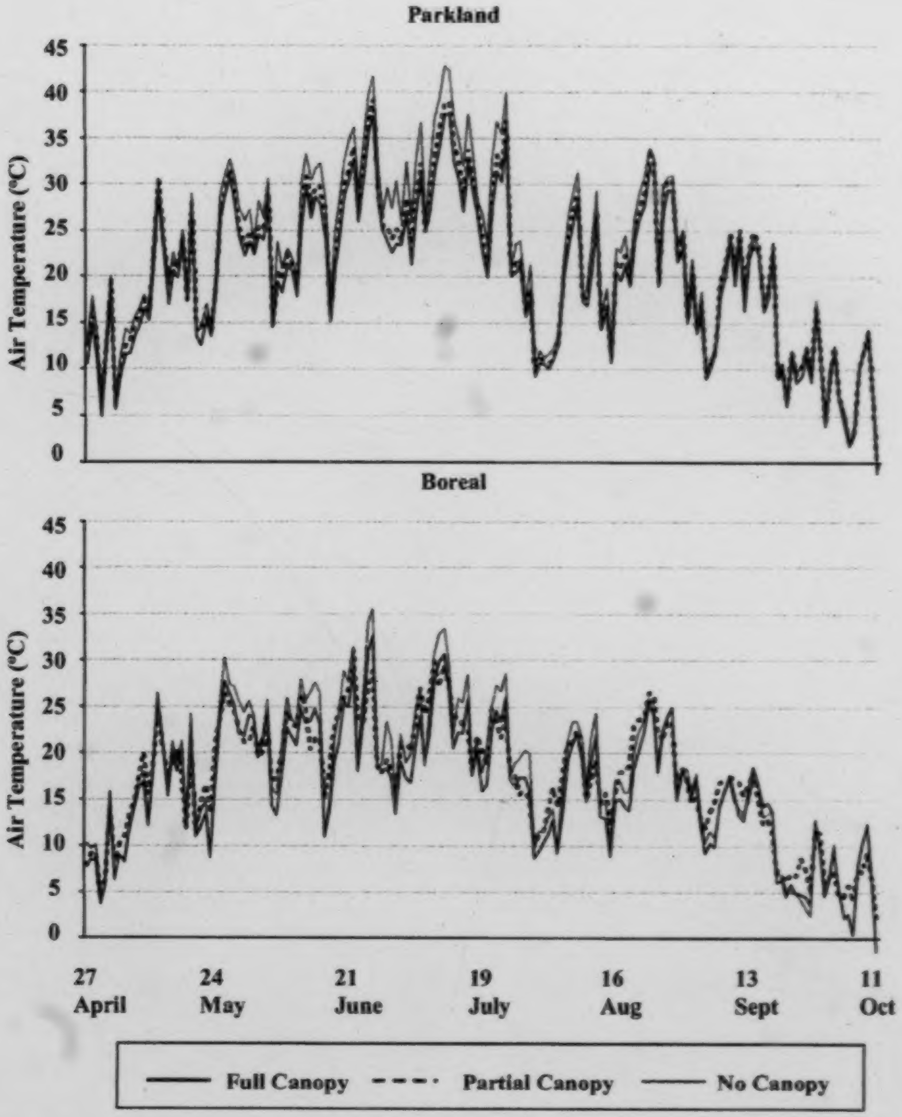


Figure 5-4 Effects of aspen (*Populus tremuloides* Michx.) canopy on daily maximum air temperature 50-cm above ground between 10 June and 1 August, 2002.

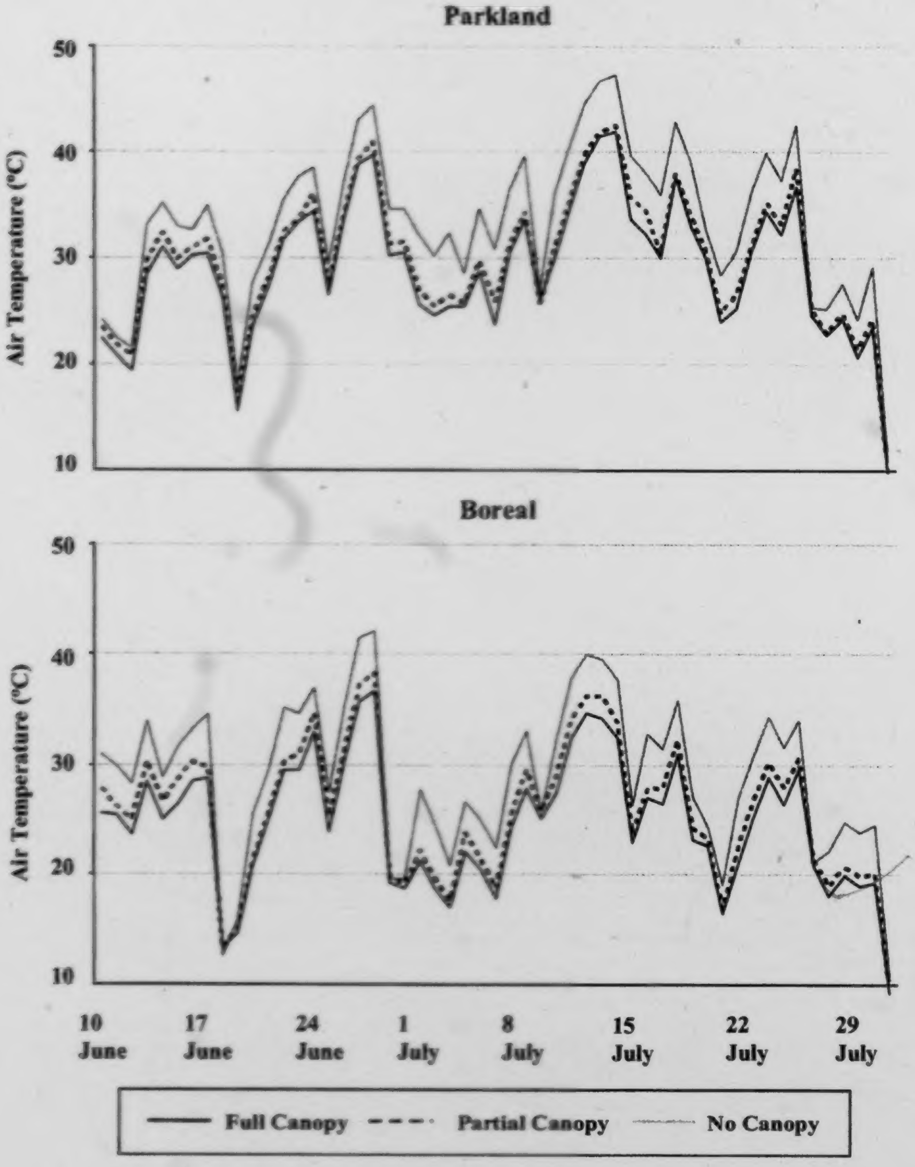


Figure 5-5 Effects of aspen (*Populus tremuloides* Michx.) canopy on daily minimum air temperature 50-cm above ground between 27 May and 23 September, 2002. Arrows indicate days on which radiative frosts (T < 0°C) occurred within plots without an aspen canopy, but did not occur with either full or partial aspen canopies.

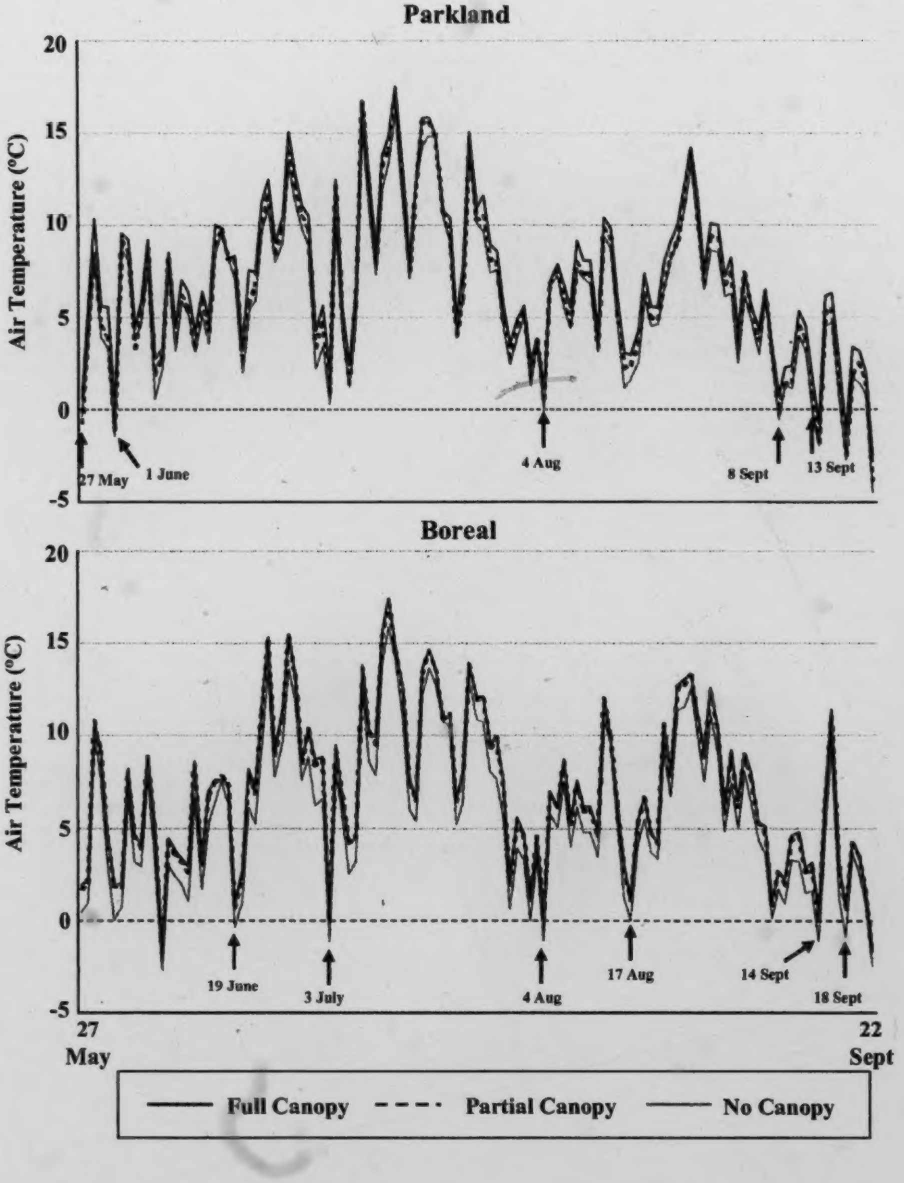


Figure 5-6 Effects of aspen (*Populus tremuloides* Michx.) canopy on annual air temperature and relative humidity at peak aspen leaf area from 2000 to 2002. Vertical lines indicate the standard errors of the least squares means.

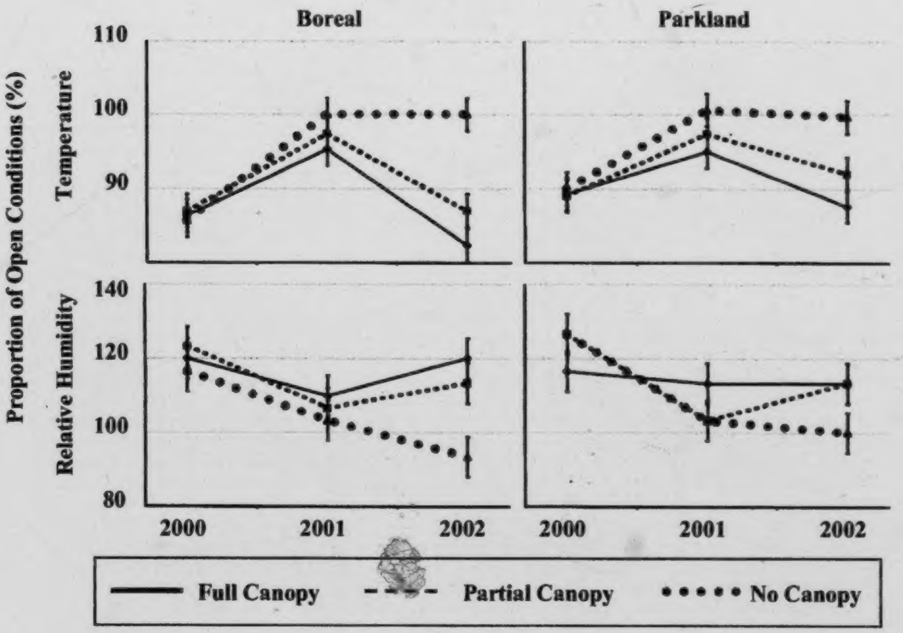


Figure 5-7 Effects of aspen (*Populus tremuloides* Michx.) canopy on daily maximum absolute humidity 50-cm above ground between 27 April and 11 October, 2002.

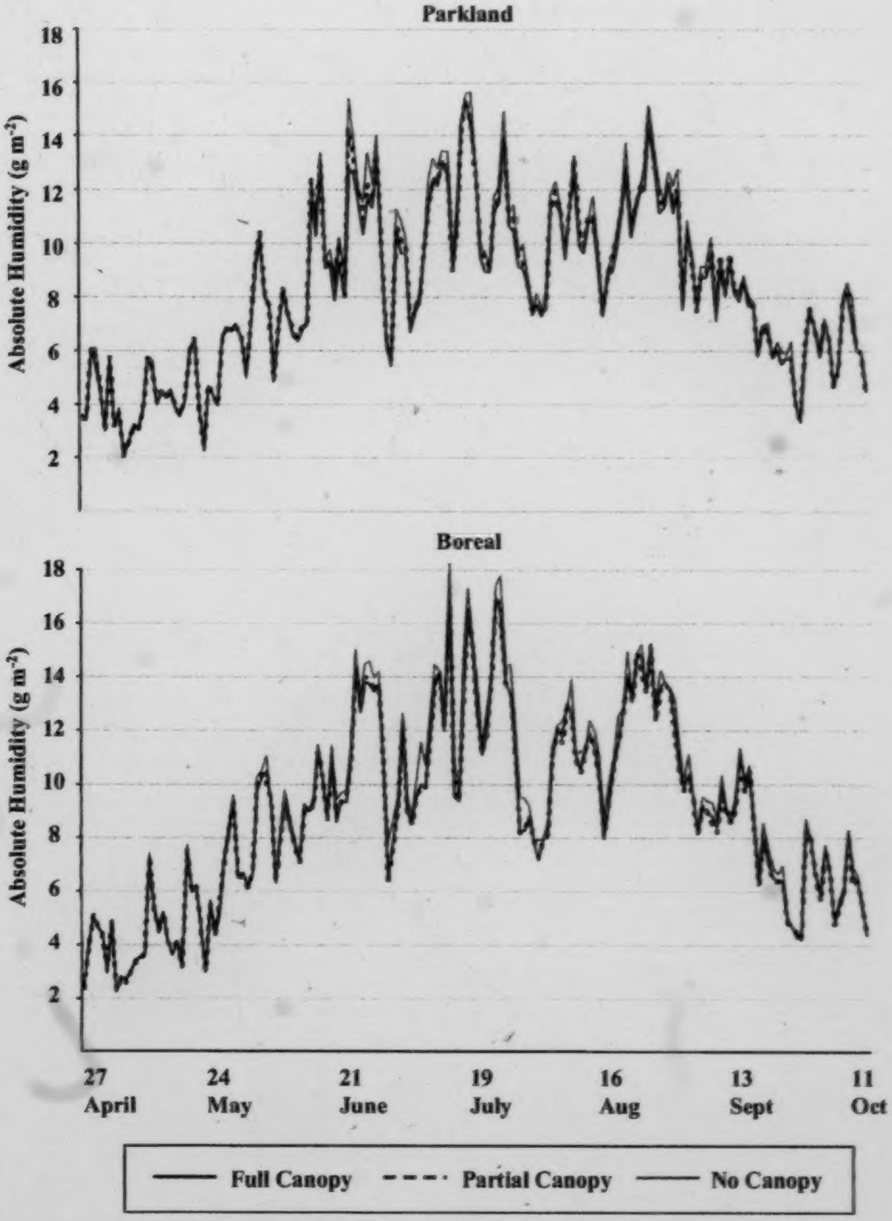


Figure 5-8 Effects of aspen (*Populus tremuloides* Michx.) canopy on average midday (13:00 to 15:00) relative humidity 50-cm above ground between 27 April and 16 July, 2002.

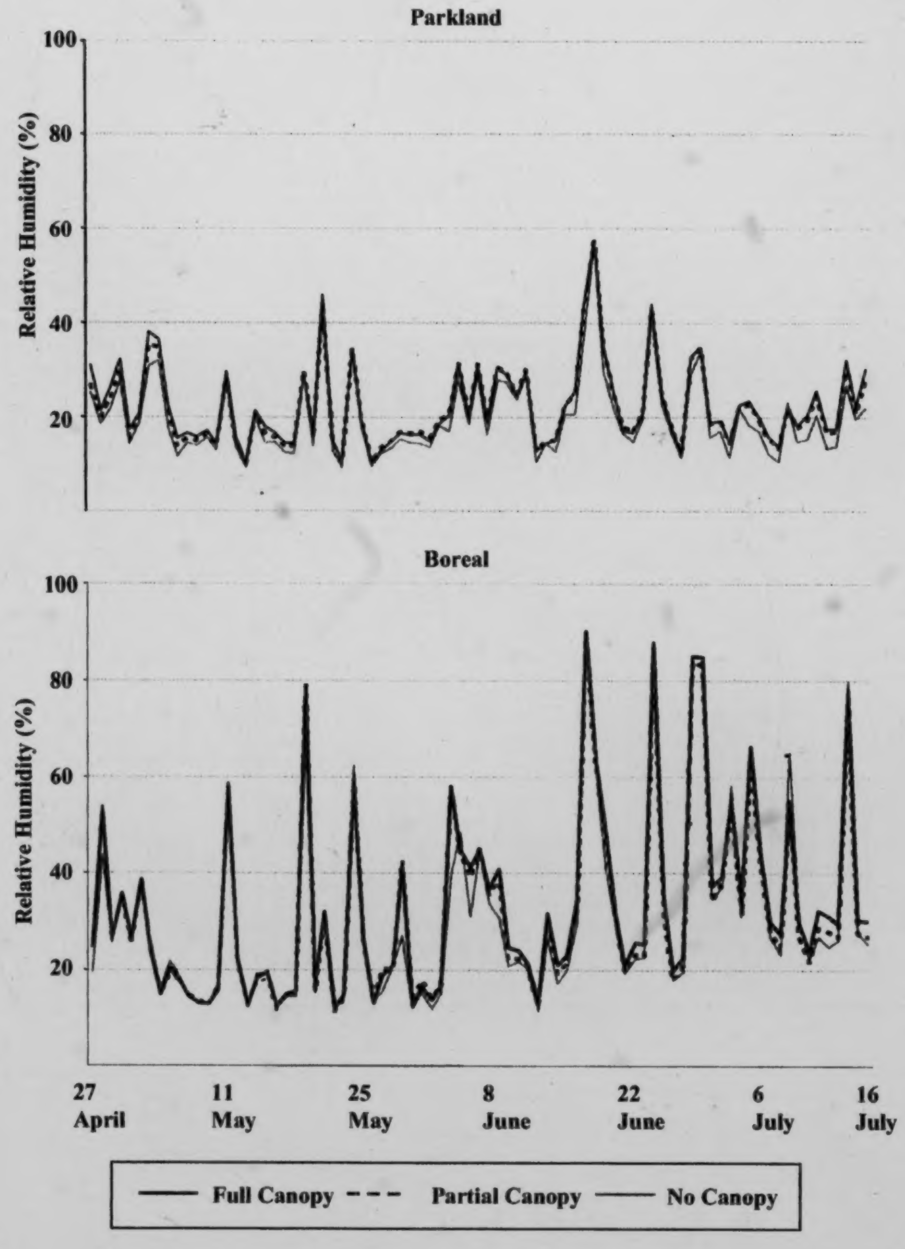


Figure 5-9 Effects of aspen (*Populus tremuloides* Michx.) canopy on the proportion of open-sky photosynthetically active radiation reaching the understory at peak aspen leaf area from 2000 to 2002. Vertical lines indicate the standard errors of the least squares means.

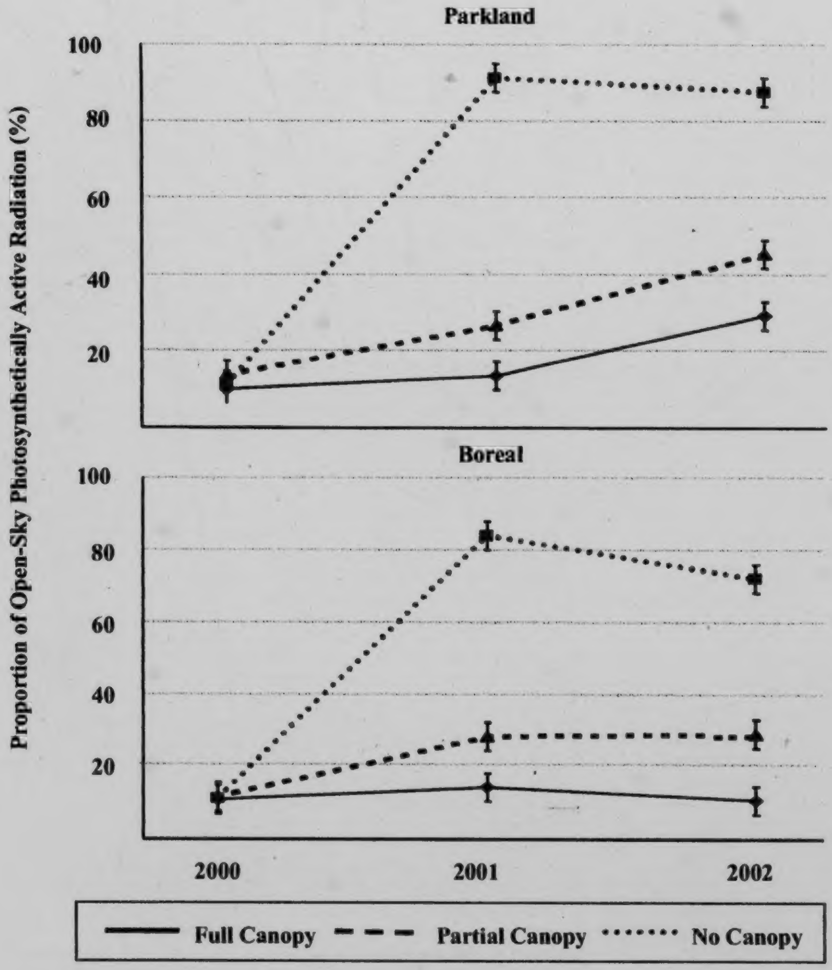


Figure 5-10 Effects of aspen (*Populus tremuloides* Michx.) canopy with root effects excluded on surface (0 to 10 cm) mineral soil water content at Parkland and Boreal sites, from May to October, 2002. Vertical lines indicate the standard errors of the least squares means.

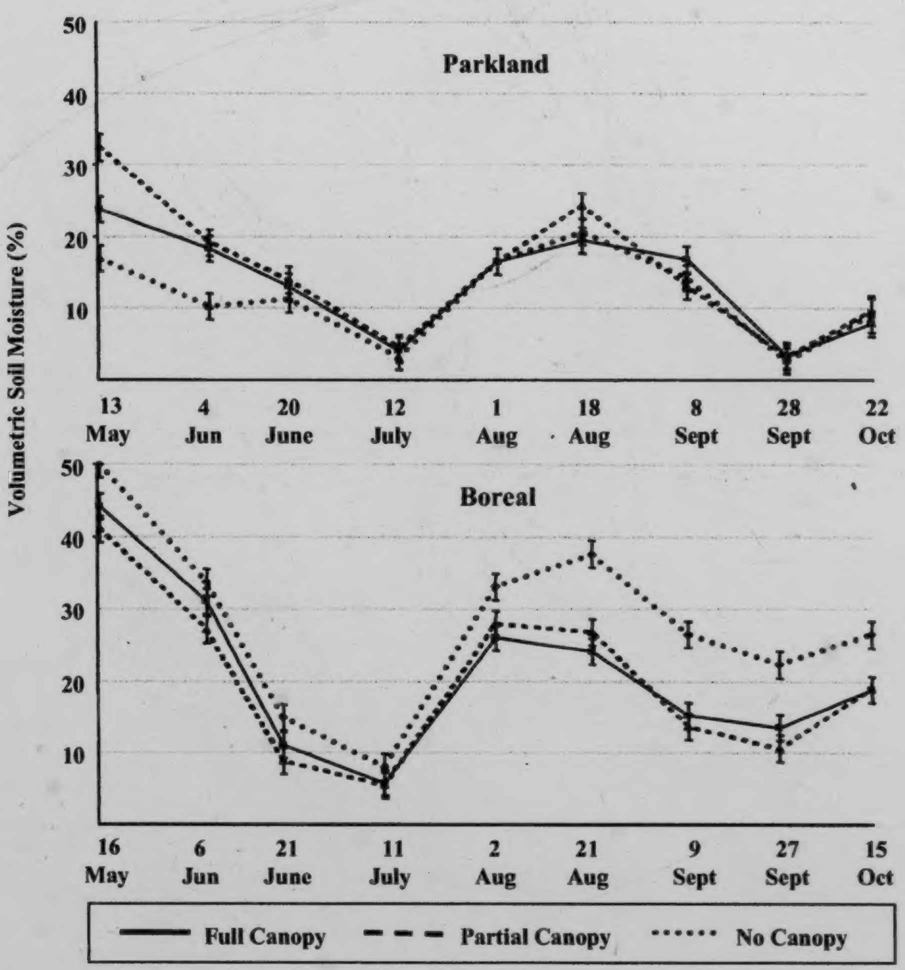


Figure 5-11 Effects of combined aspen (*Populus tremuloides* Michx.) canopy and aspen root effects on surface (0 to 10 cm) mineral soil water content at the Boreal site, May to October, 2002. Vertical lines indicate the standard errors of the least squares means.

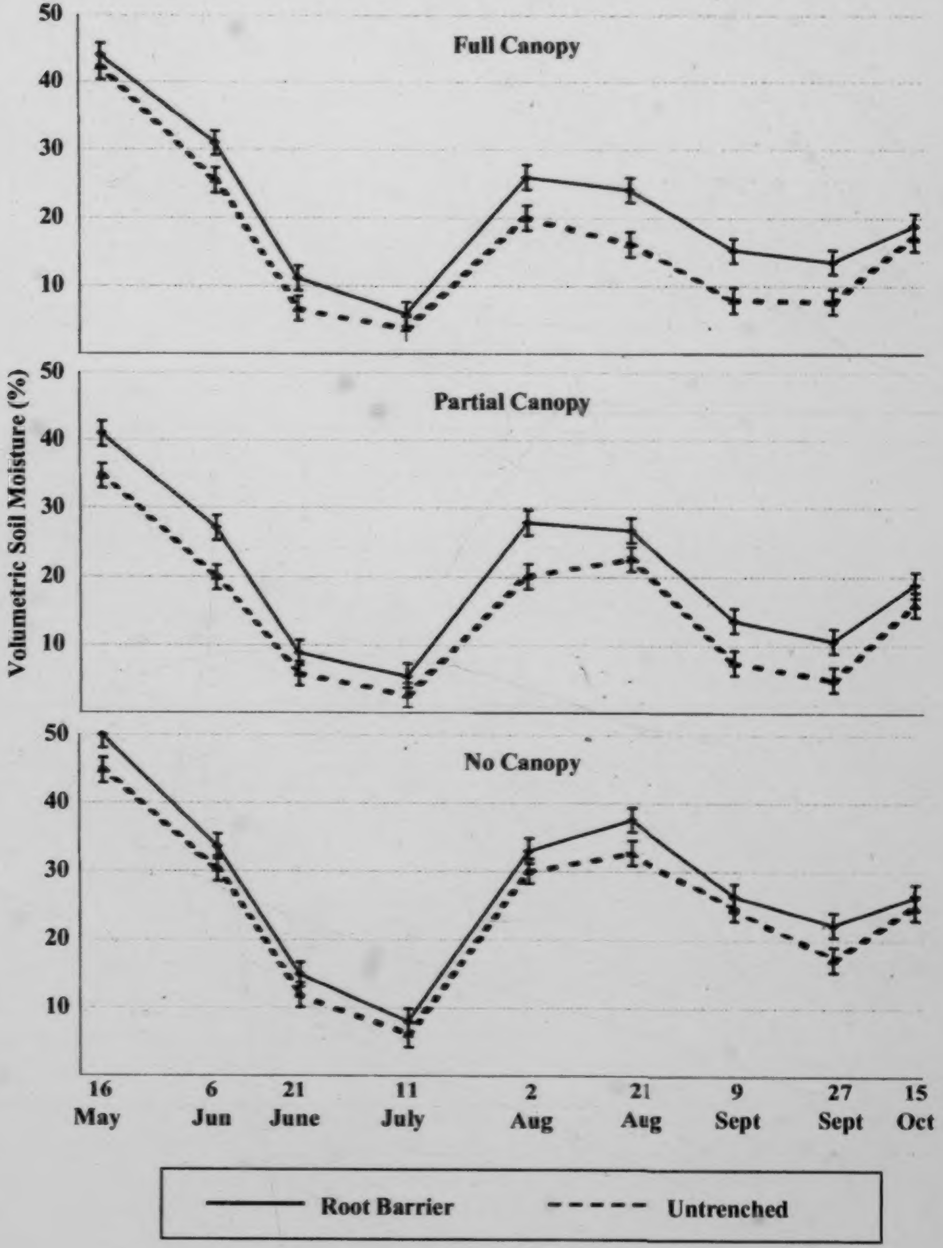


Figure 5-12 Effects of combined aspen (*Populus tremuloides* Michx.) canopy and aspen root effects on surface (0 to 10 cm) mineral soil water content at the Parkland site, May to October, 2002. Vertical lines indicate the standard errors of the least squares means.

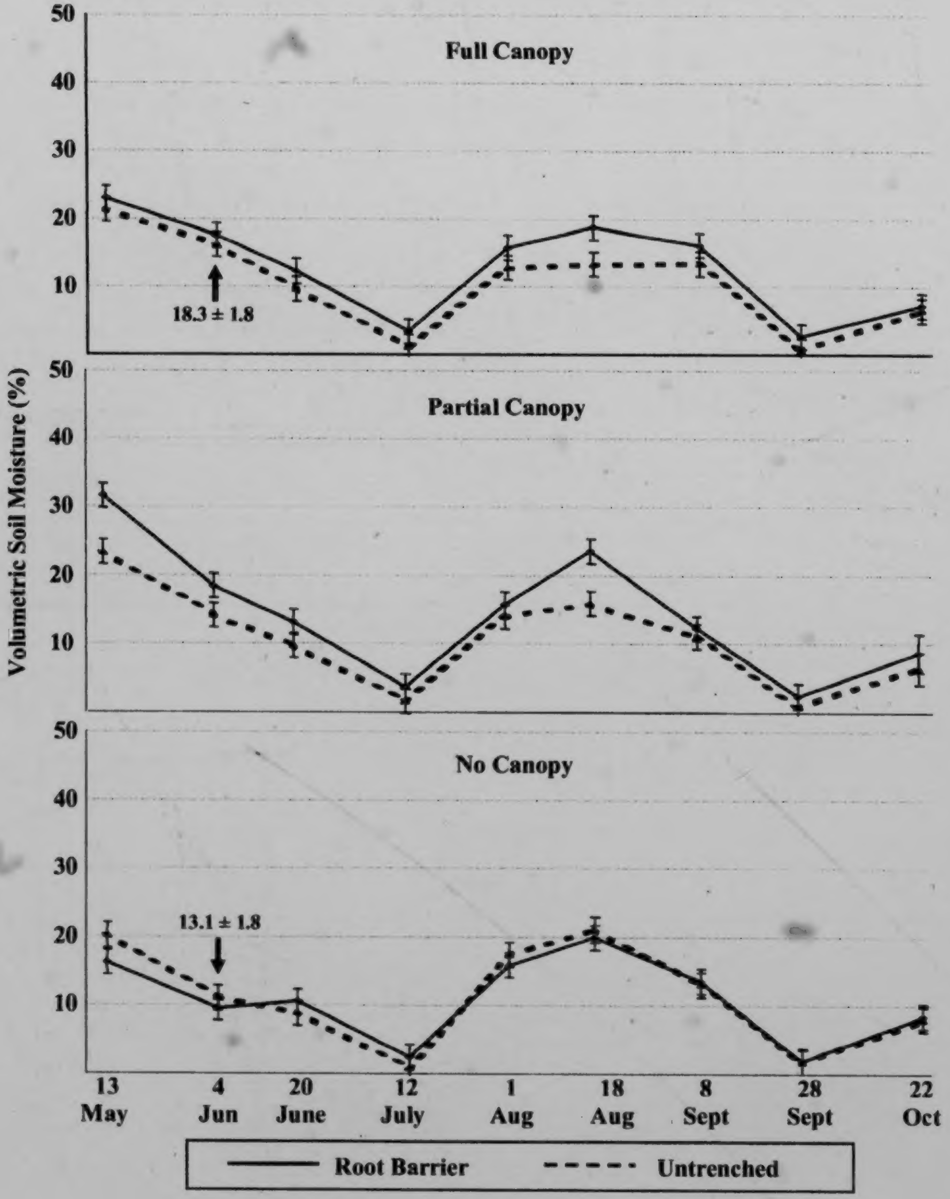
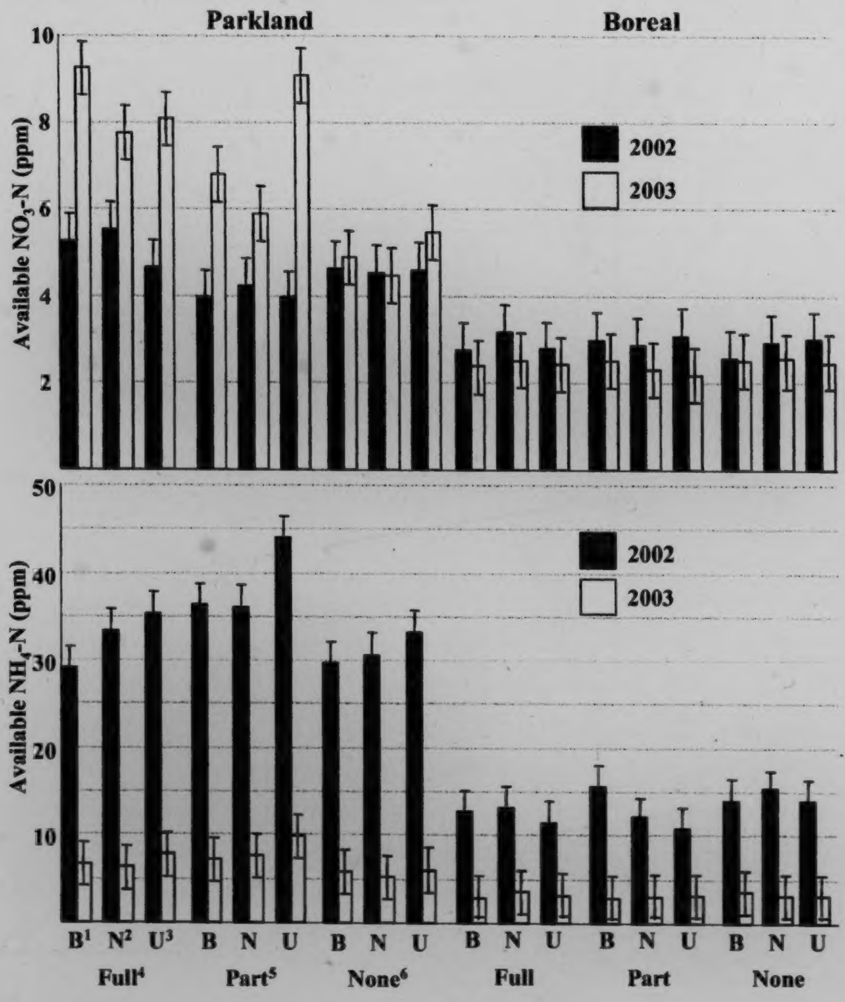


Figure 5-13 Effects of aspen (*Populus tremuloides* Michx.) canopy and root effects on available soil nitrate (NO_3-N) and ammonium (NH_4-N) at peak understory above-ground biomass in 2002, and again prior to the 2003 growing season. Vertical lines indicate the standard errors of the least squares means.



[1] Roots trenched, with plastic barrier [2] Roots trenched, no barrier [3] Roots untrenched

[4] Full aspen canopy [5] Partial aspen canopy [6] No aspen canopy

5.5 Literature Cited

Alexander, M.J. 1995. The response of mature decadent and healthy sapling aspen forest communities to prescribed burning and controlled livestock grazing. Master of Science thesis, University of Alberta, Edmonton, AB, 164 p.

Anderson, R.C., O.L. Loucks and A.M. Swain. 1969. Herbaceous response to canopy cover, light intensity and throughfall precipitation in coniferous forests. Ecology 50: 255-263.

Bertness, M.D. and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9: 191-193.

Bonan, G.B., and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecological Systems 20: 1-28.

Brenner, A.J. 1996. Microclimate modifications in agroforestry. Pages 159-187 *in*: Ong, C.K. and P. Huxley (editors). Tree-Crop Interactions: A Physiological Approach. CAB International, Cambridge, UK, 386 p.

Brooker, R.W. and T.V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos 81: 196-207.

Cannell, M.G.R. and J. Grace. 1993. Competition for light: detection, measurement and quantification. Canadian Journal of Forest Research 23: 1969-1979.

Carlson, D.W. and A. Groot. 1997. Microclimate of a clear-cut, forest interior and small openings in trembling aspen forest. Agricultural and Forest Meteorology 87: 313-329.

Coomes, D.A. and P.J. Grubb. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs 70(2): 171-207.

Dang, Q-L., H.A. Margolis, M.R. Coyea, M. Sy and G.J. Collatz. 1997. Regulation of branch level gas exchange of boreal trees: roles of shoot water potential and vapour pressure difference. Tree Physiology 17: 521-535.

Grace, J. 1983. Plant-Atmosphere Relationships. Outline studies in ecology, Chapman and Hall, New York, p 72.

Groot, A. and D.W. Carlson. 1996. Influence of shelter on night temperatures, frost damage, and bud break of white spruce seedlings. Canadian Journal of Forest Research 26: 1531-1538.

Holmgren, M., M. Scheffer and M.A. Huston. 1997. The interplay of facilitation and competition in plant communities. Ecology 78: 1966-1975.

Hogg, E.H., B. Saugier, J-Y. Pontailler, T.A. Black, W. Chen, P.A. Hurdle and A. Wu. 2000. Responses of trembling aspen and hazelnut to vapour pressure deficit in boreal deciduous forest. Tree Physiology 20: 725-734.

Jones, H.G. 1992. Plants and Microclimate, A Quantitative Approach to Environmental Plant Physiology. 2nd Edition, Cambridge University Press, Cambridge, U.K., 428 p.

Jose, S., A.R. Gillespie, J.R. Seifort and D.F. Biehle. 2000. Defining competition vectors in a temperate alley cropping system in the midwestern USA. Agroforestry Systems 48: 41-59.

Kho, R.M. 2000. A general tree-environment-crop interaction equation for predictive understanding of agroforestry systems. Agriculture, Ecosystems and Environment 80: 87-100.

Littell, R.C., W.W. Stroup and R.J. Freund. 2002. SAS® for Linear Models, Fourth Edition. SAS Institute Inc., Cary, NC, 466 p.

Man, R. and V.J. Lieffers. 1997. Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open. Tree Physiology 17: 437-444.

Marsden, B.J., V.J. Lieffers and J.J. Zwiazek. 1996. The effect of humidity on photosynthesis and water relations of white spruce seedlings during the early establishment phase. Canadian Journal of Forest Research 26: 1015-1021.

Maynard, D.G. and Y.P. Kalre. 1993. Nitrate and exchangeable ammonium nitrogen. Chapter 4, pp 25-38 *in*: Carter, M.R. (editor) Soil Sampling and Methods of Analysis. Canadian Society of Soil Science, Lewis Publisher, Boca Raton, FL, 823 p.

Oke, T.R. 1993. Boundary Layer Climates. Routledge, New York, 435 p.

Shepperd, W.D. and F.W. Smith. 1993. The role of near-surface lateral roots in the life cycle of aspen in the central Rocky Mountains. Forest Ecology and Management 61: 157-170.

Smith, D.M. 2000. Water and climatic relationships in agroforestry. Pages 115-130 *in*: Ashton, M.S. and F.M. Montagnini (editors). The Silvicultural Basis of Agroforestry Systems. CRC Press, New York, 278 p.

Strong, W.L. and G.H. La Roi. 1983. Rooting depth and successional development of selected boreal forest communities. Canadian Journal of Forest Research 13: 577-588.

Strong, W.L. and K.R. Leggat. 1992. Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife, Edmonton, AB, 59 p.

Young, D.R. and W.K. Smith. 1982. Simulation studies of the influence of understory location on transpiration and photosynthesis of *Arnica cordifolia* on clear days. Ecology 63: 1761-1770.

Young, D.R. and W.K. Smith. 1983. Effect of cloudcover on photosynthesis and transpiration in the subalpine understory species *Arnica latifolia*. Ecology 64: 681-687.

Wilson, J.R. 1990. The eleventh hypothesis: Shade. Agroforestry Today 2: 14-15.

CHAPTER 6

Effects of Aspen Canopy Removal and Root Trenching On Understory Species Composition and Production

6.1 Introduction

Ecological interactions between aspen (*Populus tremuloides* Michx.) stands and their understory can involve a complex mixture of competitive and facilitative effects (Callaway and Walker 1997) with both above- and below-ground processes. Plant-to-plant interactions are mediated through resource availability, and in forest environments resource levels are stratified and their availability in the understory depends on both the absolute amount present and the proportion available after use or modification by the overstory (Kho 2000). In agroforestry systems it is important to identify and distinguish between forms of ecological effects in order to determine the appropriate system design and management actions. Changing the balance between overstory and understory resource use in agroforests can be achieved by reducing the amount of overstory to reduce light interception by trees. However, this also reduces the tree crop and may be unnecessary if competition for water or nutrients with the overstory species is more responsible for understory yield differences than reduced light. Indeed, facilitation from overstory effects may offset the impact of reduced light. Moreover, soil resource deficits can be mitigated by fertilization or irrigation in some agroforestry systems.

Although the potential range of interactions in agroforestry systems is well defined (Kho 2000), current ecological theory does not provide a clear predictive framework for determining the specific understory response to changing above- and below-ground resource levels in northern aspen stands. Contrasting general theories predict that competition may either increase or decrease with increasing resource availability (Grime 1979, Tilman 1988). Moreover, a shift between primarily above- versus below-ground competition is theorized with changes in resource levels (Tilman 1988).

Adding to the complexity of plant community dynamics is the fact that competition and facilitation do not act in isolation of each other (Holmgren *et al.* 1997). Under a tree canopy net facilitation can occur when improved water or nutrient status 'outweighs' the 'costs' of lower light levels. Net competition occurs when the opposite is true. The balance between competition and facilitation is theorized to vary along resource gradients, with net competition expressed with increased resource availability and net facilitation occurring under "extremes" in environmental conditions or disturbance (Bertness and Callaway 1994, Brooker and Callaghan 1998, Holmgren *et al.* 1997). These predictions are based on the theories that primary productivity generally increases along gradients of decreasing stress (abiotic or disturbance), and competition intensifies with increasing productivity (Grime 1979). Furthermore, facilitation is believed to be strongest when the environmental variable being ameliorated by one plant for another is at either a high or low extremity. By this theory, facilitation is always present, but is masked by a greater impact of competition in more productive or low disturbance environments. Limited and mostly indirect evidence from field research supports the general pattern of net facilitation from an overstory under conditions of environmental extremes (Belsky 1994, McClaran and Bartolome 1989, Mueggler and Bartos 1977, Ratcliff *et al.* 1991). However, facilitation theories have not been widely tested, nor are the base assumptions and associated hypotheses universally accepted. First, there is no consensus as to whether the intensity or form of competition increases or remains constant along gradients of resource availability (Taylor *et al.* 1990), nor if there is any reason for a consistent relationship at all (Davis *et al.* 1998). Additionally, facilitation is not always expressed in "extreme" environmental conditions (Olofsson *et al.* 1999).

Previous root-shoot separation studies suggest that understory production is generally most limited by below-ground competition, with neutral or net positive effects resulting from a forest overstory. For example, root-based competition was the dominant interaction from a review of 23 greenhouse studies where root and shoot effects were separated (Wilson 1988). Likewise, 40 of 47 studies reviewed on root trenching in forest ecosystems reported a positive plant response in the species released from overstory root effects (Coombs and Grubb 2000). Ellison and Houston (1958) found greater forage production under aspen with roots trenched than under either untrenched aspen or in adjacent openings. Their results indicate that aspen root competition most limits understory production, and that an aspen overstory with root competition suppressed (through trenching) facilitates understory growth.

Unfortunately, their data are confounded because they did not trench plots without aspen canopy, and thus, those plots were still subject to root competition from shrubs and lateral aspen roots that may have extended from adjacent forest areas.

In addition to understory production changes, species composition is also an important consideration in agroforestry systems utilizing a semi-natural, polyculture of plant species (e.g. silvopastoral systems utilizing native forest vegetation). Species composition shifts in response to changing resource levels are expected, as individual adaptations to resource levels become a determining factor in both plant establishment and survival. The exact response to above- and below-ground effects however, is largely unknown. Boreal understory vascular plant diversity has shown stronger association to moisture and nutrient gradients than to light availability (Chipman and Johnson 2002), thus below-ground effects may again factor prominently in understory dynamics.

Although the majority of theoretical evidence suggests aspen understory production will be most limited by below-ground competition, previous research is predominantly from low latitude, arid ecosystems where soil moisture conservation from canopy shading supplants the negative effects of reduced light. These theories need to be tested at northern latitudes where solar input may have greater influence because of the low solar angle and shorter growing season. Sustainable integration of tree and understory crop production in northern ecosystems requires an understanding of the complex array of ecological processes affecting production. Understanding the ecological basis of agroforestry systems can ensure system design and management practices retain and enhance facilitation, while minimizing or avoiding competition.

6.2 Objectives and Hypotheses Tested

This experiment selectively reduced aspen canopy and root zone influences to determine their individual and collective effects on understory vegetation. The general objectives were to isolate and compare competitive and facilitative processes, with both above- and below-ground effects, influencing understory productivity in north temperate and lower boreal aspen stands. Specific objectives were to determine the effects of selectively removing aspen canopy and root effects on the understory species composition and production. The following null hypotheses were tested:

1. aspen canopy removal has no effect on remaining aspen height or basal area;
2. aspen canopy removal has no effect on understory species composition or production;
3. root trenching under aspen has no effect on understory species composition and production; and,
4. the interaction of aspen canopy removal and root trenching has no effect on understory species composition and production.

6.3 Methods

Research Sites

Research was conducted at two sites in central Alberta containing juvenile (15-20 year old) aspen stands. The first site ('Boreal') was located in the Lower Boreal Mixedwood natural region (Strong and Leggat 1992) southwest of Lac La Biche, Alberta (54° 33' N, 112° 05' W) on the Lakeland Agricultural Research Association lease. The Boreal site receives 504 mm of precipitation annually with approximately half during the growing season (1970-2000 normal, Environment Canada). Aspen at the Boreal site at the beginning of the experiment were 18-20 years old, at an average density of 16,319 ± 367 stems ha^{-1}, height of 5.7 ± 0.2 m, and basal area of 22.7 ± 1.7 m^2 ha^{-1}. Native shrubs and forbs including low-bush cranberry (*Viburnum edule* (Michx.) Raf.), prickly rose (*Rosa acicularis* Lindl.) and wild sarsaparilla (*Aralia nudicaulis* L.) dominated the understory vegetation at the beginning of the experiment.

The second site ('Parkland') was located in the Aspen Parkland natural region, north of Kinsella, Alberta (53° 00' N, 111° 32' W) on the University of Alberta's Research Ranch. The Parkland site was situated on well-drained, glaciolacustrine sediments and receives 431 mm of precipitation annually with more than 70% during the April to September growing season (1970-2000 normal, Environment Canada). Aspen at the Parkland site at the beginning of the experiment were 15-18 years old, at an average density of 13,194 ± 1,696 stems ha^{-1}, height of 6.3 ± 0.2 m, and basal area of

25.4 ± 1.7 m^2 ha^{-1}. Understory vegetation was dominated by native shrubs, principally western snowberry (*Symphoricarpos occidentalis* Hook.) and prickly rose, and a mixture of native and introduced grasses, including smooth bromegrass (*Bromus inermis* Leys).

Treatments and Experimental Design

Nine, 10- x 10- m macroplots were selected at each site for relative uniformity of aspen density and size, topography, slope and aspect to minimize the potential confounding effects of these variables. Treatments were applied in a split-plot design. Three levels of aspen canopy removal were randomly applied three times each to macroplots (main plots) by cutting the appropriate number of aspen stems off at ground level. The following canopy removal treatments were tested:

1. no aspen canopy removal (control);
2. partial canopy removal (equal to the amount necessary to increase insolation by approximately 100%); and,
3. full aspen canopy removal.

Partial canopy removal was conducted such that remaining stems were approximately equidistantly spaced and evenly dispersed across the macroplots, with an average post-thinning density of 6,770 ± 640 stems ha^{-1}. Aspen stems cut for the canopy removal treatments were removed from the macroplots. Macroplots were set a minimum of 5-m apart, as well as a minimum of 5-m from major openings or atypical site conditions to minimize edge effects around the treatment units. Resprouting (suckering) aspen originating from the roots or stem base of treated areas were removed biweekly during the aspen growing seasons.

Within each macroplot, three root trenching treatments were applied on 0.5- x 2.0-m (1 m^2 area) rectangular subplots in the centre of the aspen canopy removal macroplots (Figure 5-1, Chapter 5). The following treatments were applied to the subplots:

1. trenched with a root barrier;
2. trenched and no barrier control; and,
3. untrenched control.

Each root trenching treatment was applied twice in each macroplot, for a total of six subplots per macroplot. To minimize potential edge effects from the macroplots on the root trenching treatments, a 3-m buffer was established between the outside edge of the subplots and perimeter of the macroplots. Subplots were randomly assigned to one of eight positions within the centre of the macroplots inside the inner bound of the buffer, with 50-cm buffers between subplots (Figure 5-1, Chapter 5). Subplots requiring trenching were trenched 5-cm wide to a depth of 40-cm. This depth is below the main surface roots of aspen and accompanying understory vegetation (Strong and La Roi 1983). The 'trenched with barrier' plots were lined with two layers of 6-mil (150 μm) clear plastic sheeting to prevent regrowth of aspen roots into the subplots.

Measures

Photosynthetically active radiation (PAR), air temperature (T), relative humidity (RH), soil moisture and available soil nitrate (NO_3-N) and ammonium (NH_4-N) were measured. Methods employed, and more detailed results and discussion of the microclimate and soils are reported in Chapter 5, this volume.

Aspen height was estimated with a clinometer to the nearest 0.5 m, and diameter at breast height (DBH, 1.3 m above ground level) was measured to the nearest 0.1 cm. Height and DBH measures were conducted annually on individually tagged aspen stems (n=17 to 29) within the inner buffer of each macroplot bounding the root trenching subplots (Figure 5-1, Chapter 5). Basal area (BA) was calculated from tree diameter measures for each stem prior to treatment in 2000, and again in October 2002. Basal area increment (BAI) was calculated from the difference in these BA measures. Quadratic mean tree diameter (QMD) for each macroplot was calculated from DBH in each sampling period. Relative diameter growth (RGR_D) was calculated on each tree by dividing the change in DBH from end to beginning of the experiment, by the DBH at the beginning period. Aspen density (SPH) was determined as the number of aspen stems greater than 2-m tall within each macroplot. Height growth was calculated on each tree from the differences between baseline sampling to experiment completion. Relative height growth (RGR_H) was calculated on each tree by dividing height growth by the height at the beginning period. Resprouting (suckering) aspen originating from aspen roots or stem bases in treated macroplots were removed and counted periodically throughout the experiment.

Understory cover and production estimates were conducted annually at the presumed peak standing crop of biomass (late July to early August of each year). Understory species composition and cover were determined from nested quadrats within the root trenching subplots. Herbaceous vegetation and aspen leaf litter were estimated by averaging ocular estimates of canopy-coverage to the nearest 2% on two randomly located, 10- x 50- cm quadrats per subplot (Daubenmire 1959). Shrubs were separated by size into two strata; the cover of shrubs greater than 1-m tall ('tall shrubs') was estimated to the nearest 5% over the entire 1-m^2 root-trenching subplots, whereas the canopy-cover of shrubs less than 1-m tall ('low shrubs') was estimated in the 10- x 50-cm frames used for herbaceous plant cover. Cover of plant groups (forbs, graminoids, low shrubs, tall shrubs) was calculated by summing the cover of the individual species comprising these groupings.

Simpson and Shannon diversity indices were calculated using cover data for the measure of species abundance in the indices (Magurran 1988). Simpson's index (D) was calculated using the formulas:

$$D = \Sigma (p_i)^2$$

$$p_i = n_i N^{-1}$$

where 'n_i' is the cover of an individual plant species and 'N' is the total cover of all plant species in each plot. The reciprocal of Simpson's index (D^{-1}) is reported for clarity (i.e. a larger value of D^{-1} corresponds to a larger measure of diversity). Shannon diversity (H) was calculated using the formula:

$$H = -\Sigma p_i (\ln p_i)$$

Species density (Hurlbert 1971) was calculated as the average number of vascular plant species in each canopy removal - root trenching treatment combination.

Above-ground net primary production (ANPP) was estimated annually by clipping a 0.25-m^2 area to ground level in each root trenching subplot at the presumed peak standing biomass. Current year's growth was separated from litter and divided into three groups: shrubs, graminoids and forbs. All samples were dried at 70 °C to constant mass (to the nearest 0.1 g) and weighed. Relative yields were calculated by determining the proportion of total annual production contributed by each of the three plant groups.

Except where otherwise noted, all measures were conducted over three growing seasons. Baseline measures were conducted prior to treatment application from May to early August 2000. Plots were sampled annually for two more consecutive years (2001 and 2002) after the thinning and trenching treatments were applied in September and October of 2000. Sample locations within subplots were selected with a restricted randomization. Understory canopy cover quadrat locations were located randomly and the same plot location was sampled each year. Destructive sampling for determining ANPP was restricted to the remainder of the root trenching subplot area on which cover estimates were not conducted. Production sample locations were re-randomized to a new location within a given subplot in each year to ensure sampling in the latter years were not biased by previous biomass removal.

Analyses

Effects of canopy removal on tree BAI, height growth, RGR_H and RGR_D were assessed with an analysis of variance using mixed models (Table A2-13, Appendix 2, Littell *et al.* 2002). Annual measures of tree SPH, BA, QMD, height as well as understory ANPP, cover and diversity measures were analyzed with repeated measures, mixed linear models (Tables A2-14 and A2-15, Appendix 2). The absolute difference in the relative yield of understory plant groups was analyzed with a multivariate analysis of variance (MANOVA) for a split-plot design (Table A2-16, Appendix 2).

Data were checked for normality and homogeneity of variance and most met these assumptions for parametric analyses. Square-roots were taken of the forb cover data, and graminoid cover and aspen regeneration data were transformed with a natural logarithm (datum +1) to obtain a normal distribution of the residual errors. Kenward-

Roger corrections were applied to the degrees of freedom in the mixed models analyses to overcome any sample size bias. Differences between specific canopy and root trenching treatments were determined with individual degree of freedom contrasts. Sites, canopy removal and root trenching treatments were assumed to have fixed effects; variation between treatments (assessed with replication) was assumed to introduce random effects. The covariance models used in the repeated measures analyses were selected iteratively for each response variable by testing several structures and comparing Schwarz's Bayesian information criterion. This test is based on the maximum likelihood fit corrected for the number of parameters in the model, analogous to the adjusted R^2 employed in multiple regression analyses. Covariance between sampling periods for all measures of cover and diversity were unstructured. Covariance for total, forb and graminoid ANPP were also unstructured, however shrub ANPP, aspen SPH, BA and suckering data displayed compound symmetry.

Annual measures of PAR at peak aspen leaf area were regressed against ANPP and cover measures. Understory canopy cover and ANPP in 2002 were regressed against a more complete set of environmental parameters (PAR, soil moisture at several time periods, NO_3-N and NH_4-N). Regressions of the multiple independent variables were conducted using a forward stepwise technique to find the combination and order of variables that produced the best-fit model for the 2002 data. Plots of the residual values from the regression equations against their expected values indicated linear models were appropriate for the analyses. The proportion of open-sky PAR reaching the understory was regressed against aspen SPH and BA on each macroplot across all sampling periods. Data were tested against various curves (linear, quadratic, natural and base-10 logarithms) to determine the best fit model.

6.4 Results and Discussion

Aspen Growth and Stand Characteristics

Pre-treatment BA did not differ ($p=0.50$) between sites, while SPH was greater ($p<0.01$) at the Boreal site than the Parkland site (Figure 6-1). However, the density of dominant and codominant trees (≥5.5-m tall) did not differ ($p=0.25$) among the sites (average

9,444 ± 386 stems ha^{-1}), indicating the SPH differences resulted from a higher number of suppressed (<5.5-m tall) stems at the Boreal site. Predictably, removal of aspen stems in the partial canopy treatment resulted in significantly lower ($p<0.0001$) SPH and BA ($p<0.0001$). Pre-treatment BA values at both sites fall within the range reported for 14 to 25 yr-old boreal aspen stands (Comeau 2001).

Stand densities remained stable after the prescribed stem removal at the Boreal site, but decreased ($p<0.01$) in the full aspen canopy treatment in 2002 at the Parkland site (Figure 6-1). Mortality of suppressed aspen was responsible for the decrease in SPH at the Parkland site, likely resulting from the severe drought conditions early in the 2002 growing season (see Chapter 5, this volume, for a detailed description of the weather patterns during the study). The decrease in SPH corresponded to an increase in PAR penetration under the full aspen canopy at the Parkland site during the 2002 growing season (see Chapter 5, this volume). Despite the decrease in SPH, stand BA did not decline significantly at the Parkland site with no post-treatment BA differences between years ($p=0.59$) or sites ($p=0.50$). In fact, there was a trend towards greater total BA in both partial and full canopy treatments resulting from aspen growth over that period (Figure 6-1). Because mortality at the Parkland site was predominantly smaller, suppressed trees, it had less impact on BA than SPH.

Stand density ($r^2=0.81$, $p<0.0001$) and BA showed strong ($r^2=0.71$, $p<0.0001$) negative linear relationships to the portion of open-sky PAR in the understory (Figure 6-2). The relationship of PAR to SPH was marginally improved by a quadratic transformation of PAR data ($r^2=0.83$, $p<0.0001$), however the correlation to BA decreased ($r^2=0.69$, $p<0.0001$) with the same. The negative relationship observed between PAR and aspen stand parameters are not as strong as reported elsewhere (Comeau 2001, Messier *et al.* 1998), possibly due to less direct correlation between aspen leaf area and BA in the Parkland where drier conditions influence leaf development, coupled with the wider range of BA and light conditions from which the other models were developed.

Aspen stand BAI from 2000 to 2002 did not differ among sites ($p=0.18$) or canopy removal treatments ($p=0.31$). Average BAI per stem ($p>0.25$) and RGR_D ($p>0.40$), were similarly unaffected by aspen removal treatments (Table 6-1). However, there was a trend towards greater BAI ha^{-1} with full aspen canopy at both sites, as would be expected from the larger number of trees contributing to stand growth in this treatment.

Moreover, there was a trend of greater RGR_D among the remaining aspen in the partial canopy removal treatment, in keeping with conventional theories on the relationship of plant size to density. The thinning method employed for creating the partial canopy treatment ('thinning from below') removed a higher proportion of small trees. This resulted in a nominal (non-significant) post-treatment increase in both the average QMD and height in the partial canopy treatment as a mathematical consequence of removing small trees from the stand averages (Figure 6-1). Coupled with the trend towards improved tree growth in the partial canopy treatment, this resulted in taller ($p<0.0001$) and larger diameter ($p<0.0001$) trees over the course of the experiment at the Boreal site, but not at the Parkland site. Moreover, overall there was better height growth ($p=0.04$) and RGR_H ($p=0.06$) with a partial canopy, and both height growth measures were greater ($p=0.02$ to 0.03) at the Boreal site than the Parkland site (Figure 6-1).

As has been widely observed elsewhere (Peterson and Peterson 1992), aspen vegetative regeneration increased exponentially ($p<0.0001$) with aspen removal (Figure 6-3) with significant differences ($p<0.01$) between all treatments in all sampling periods. Cumulative suckering response was nominally the greatest at the Parkland site with complete canopy removal, but did not differ significantly ($p=0.33$) between sites. Because all aspen regeneration was removed as it emerged, it likely only had minor and transient effects on understory vegetation dynamics.

Above-ground Net Primary Production

No differences existed ($p>0.10$) in understory production with the baseline measures of 2000, however, total ANPP was greater on average at the Parkland site ($p<0.0001$), and showed strong multi-year responses to canopy removal ($p<0.0001$) and root trenching ($p=0.04$) at both sites (Figure 6-4). The timing and nature of the treatment effects however, differed between sites with an interaction of site with both canopy ($p=0.03$) and trenching ($p=0.03$) effects.

In 2001 ANPP at both the Parkland ($p=0.02$) and Boreal ($p=0.06$) sites increased with aspen canopy removal (Figure 6-4). At the Parkland site, ANPP was lower under a full canopy than on either partial ($p=0.04$) or complete ($p<0.01$) canopy removal plots. Aspen overstory had the same effects at the Boreal site, with ANPP lower under a full canopy than on either partial ($p=0.06$) or complete ($p=0.03$) canopy removal plots (Figure 6-4). In contrast, ANPP responded differently to root trenching between the two sites in 2001. Root trenching did not influence ANPP ($p=0.20$) at the Parkland site, but did increase production at the Boreal site ($p<0.01$) where it also exhibited an interaction with canopy removal ($p<0.01$). Trenching with a barrier in place increased ANPP relative to either trenching without a barrier ($p<0.0001$) or the untrenched control ($p<0.001$) at the Boreal site, but only with complete canopy removal (Figure 6-4).

In 2002, aspen cover continued to have strong effects on ANPP at both the Parkland ($p<0.01$) and Boreal ($p<0.001$) sites. Production increased with decreasing aspen overstory at the Boreal site with a distinct difference ($p<0.01$ to 0.04) between all canopy treatments (Figure 6-4). In contrast, ANPP at the Parkland site was lower under a full canopy than either partial ($p=0.02$) or complete ($p<0.01$) canopy removal, but biomass production under the partial canopy did not differ ($p=0.13$) from that of complete canopy removal (Figure 6-4). Moreover, although there were no overall trenching effects at either site in 2002 ($p>0.15$), ANPP differed ($p<0.05$) within some canopy-trenching combinations. The Boreal site showed the same trenching response as was expressed in 2001; with complete canopy removal, greater ANPP resulted from trenching with a barrier in place than either trenching without a barrier ($p=0.03$) or the untrenched control ($p=0.05$). In contrast, trenching treatments were generally masked by larger subplot variability at the Parkland site. However, within the partial canopy removal treatment, ANPP was greater ($p=0.06$) with either trenching technique than the untrenched control (Figure 6-4).

Production of individual vegetation groups displayed greater site and interannual variability than total ANPP, and as a consequence showed fewer significant trends relative to the treatments. In general, forb ANPP mirrored the response of total ANPP to aspen canopy and root trenching treatments, but with somewhat lower significance and a non-significant trend of decreased production under the partial canopy at the Parkland site (Table 6-2). Shrub ANPP was greater on average at the Boreal site ($p<0.01$) than at the Parkland site, and increased ($p<0.0001$) across all site and treatment combinations between 2000 and 2002. Aspen canopy ($p=0.08$) and root trenching ($p=0.61$) treatments however, did not influence shrub ANPP (Table 6-2). Graminoid ANPP displayed the strongest responses to aspen canopy and root modification. Graminoid ANPP was initially greater ($p<0.0001$) at the Parkland site and remained so throughout the experiment (Table 6-2). Aspen canopy had a multi-year effect on graminoid ANPP ($p<0.01$), but this response varied annually within combinations of site and canopy treatments ($p=0.01$). Parkland site graminoid ANPP increased ($p=0.03$) with complete canopy removal relative to a full aspen canopy in 2001, and was greater with either full ($p=0.02$) or partial canopy ($p=0.04$) removal than the unthinned controls in 2002. At the Boreal site, canopy removal only produced significant differences ($p<0.001$) in graminoid ANPP two years after canopy removal, when graminoid ANPP was greater without a tree overstory than under either the full ($p<0.001$) or partial ($p<0.01$) aspen canopies. Root trenching did not ($p=0.36$) produce an overall effect on graminoid ANPP, although trenching with a barrier in place produced 2.4 times greater ($p<0.01$) ANPP than the other trenching treatments when combined with complete canopy removal in 2002 at the Boreal site. Moreover, the same trend (though not significant) of greater graminoid ANPP with trenching and barrier in place was evident under a full canopy.

Relative Yield

A difference in understory ANPP between sites was also evident in how different plant groups contributed to total production. Apart from one anomaly at the Boreal site (full canopy, untrenched control), there was a common trend in the change in relative yield at both sites in that the magnitude of change was similar within canopy treatments across sites (Figure 6-5). In agreement with the ANPP data however, shifts in vegetation groups contributing to total yield were different ($p=0.02$) between sites. At the Parkland site, with full or partial canopy removal, there was an approximately equivalent shift ($p<0.001$) away from both forb and shrub production towards a greater proportion of graminoids. At the Boreal site, partial canopy removal resulted in proportionately more of total ANPP derived from shrubs ($p<0.001$). With complete overstory removal at the Boreal site there was a shift towards greater production contributions from the graminoid species, and that response was strongest with root trenching using a barrier (Figure 6-5). In contrast, Bartos and Mueggler (1982) found little change in understory relative yield three years after clearing mature aspen.

Understory Production During Drought

Production within the unthinned controls did not differ from 2000 to 2001 at either the Parkland ($p=0.21$) or the Boreal sites ($p=0.69$). During the most severe drought event ever recorded for these areas, however, ANPP under the full canopy plots in the Parkland site in 2002 increased ($p<0.0001$) over the levels observed under more normal conditions in the previous two years. Moreover, although not significant ($p=0.09$), the same trend of increased understory ANPP in the full canopy treatment was evident at the similarly drought affected Boreal site.

Three mechanisms, alone or in combination, may have contributed to this paradoxical production increase during drought. First, it may reflect a time-delayed effect from the elimination of domestic animal herbivory resulting from fencing the research sites after the treatments were applied. This is unlikely however, because prior to treatment all plots were generally inaccessible to large animals because of the high density of aspen, and moreover, no herbivory or animal sign was noted on the ANPP plots during the pre-treatment sampling. Light herbivory and animal sign was noted in natural openings at both sites, but experimental plots were not placed on those locations. Thus, grazing likely had very little influence on pre-treatment production.

Alternately, the ANPP increase may have resulted from nutrients released with the death of suppressed aspen (an Assart effect). Commonly referred to as a 'nutrient flush,' this response is observed on recently cut-over or burnt forestland where soil nutrients held in suspension by the transpiration pull, or trapped in fine roots are released from dead trees. However, while this effect may have influenced understory ANPP, drought conditions dictate that the effects would most likely have been small. The lack of soil moisture would have greatly restricted movement of mobile nutrients in the soil. Moreover, the clonal nature of aspen would have ensured some nutrients held in the suppressed aspen would have been reabsorbed by the clone, and any released to the soil would be competitively partitioned between understory species and remaining aspen.

A third possible mechanism for understory production increases during drought may be more favourable microclimatic conditions than under more mesic weather patterns. Aspen stem mortality, possibly combined with less leaf area produced on surviving aspen, resulted in a higher proportion of PAR reaching the understory in 2002 than the previous two years (see Chapter 5, this volume). This was coupled with a net increase in soil moisture under the aspen during the drought at the Parkland site (see Chapter 5, this volume). Therefore, growing conditions experienced by the understory within the drought period were possibly better than when aspen are growing more vigorously. Under normal precipitation regimes, forage production under Parkland aspen can be 50 to 90 % lower than adjacent grassland sites (Paulsen 1969, Bailey and Wroe 1974), attributable to both inherent production differences of the dominant herbaceous species present and growth suppression in the aspen understory. It has been casually observed however, that during droughts, understory productions levels are often buffered from full drought effects. Likewise, Hilton and Bailey (1974) recorded an increase in understory production in the Parkland during a drought in comparison to a year of normal precipitation. In their study production under small aspen (DBH < 8 cm) increased from 310 to 485 kg ha^{-1}, and production under large aspen (DBH > 8 cm) increased from 110 to 123 kg ha^{-1} in the control (untreated) plots of an experiment testing chemical control of young aspen stands. The authors did not attribute the production increases to additional resources available under drought stressed aspen, but rather, believed they had biased the placement of their control plots to unusually productive areas of the understory.

Understory Species Composition and Canopy Cover

Understory species composition trends generally follow the pattern of changes observed in ANPP relative to aspen canopy removal and root trenching. Three cover components displayed strong pre-treatment site differences. There was greater wood debris (p<0.0001) and tall shrub cover (p<0.0001) at the Boreal site, and greater graminoid cover at the Parkland site (p<0.0001) at the beginning of the experiment. Wood cover averaged 0.2, 1.5 and 2.5% at the Parkland site from 2000 to 2002, respectively and did not vary with canopy or root trenching treatments in 2001 (p>0.10). Wood cover was 3% (absolute) greater (p=0.04) at the Parkland site with a full canopy than with complete aspen removal in 2002, a result of stem and branch fall originating from the aspen mortality that year. Wood cover averaged 11.8, 10.6 and 13.9% at the Boreal site and did not differ significantly (p>0.15) between years or treatments.

Tall shrub cover displayed the greatest relative spatial difference between sites of the vegetation components, with infrequent large shrubs distributed at the Parkland site and a greater, more evenly distributed cover at the Boreal site (Table 6-3). Tall shrub cover was unaffected by canopy removal and root trenching at the Parkland site throughout the experiment (p>0.5). At the Boreal site, canopy removal initially reduced tall shrub cover (p<0.01). This resulted from both the canopy removal treatment technique and the growth nature of one species. As a matter of practicality and safety, tall shrub stems in close proximity to tree stems were cut in the process of removing aspen cover. Moreover, the tall shrub twining honeysuckle (*Lonicera dioica* L.) uses tree stems for growth support and therefore the removal of aspen cover directly reduced its habitat (see Appendix 3 for detailed tabulations of individual species' canopy cover). Shrub regrowth likely negated differences (p=0.26) between canopy treatments at the Boreal site in 2002. Despite the unequal tall shrub distribution, a test of tall shrub cover as a covariate with the canopy cover and ANPP of the other plant groups did not generate significant results (p>0.25), and therefore, was omitted from the analytical models.

Low shrub cover (shrubs <1-m tall) was the most stable understory cover component and the only treatment responses observed were due to root trenching. Low shrub cover did not differ (p=0.15) between sites nor did it respond to aspen canopy removal (p=0.22). In the year following treatment, trenching with or without a barrier in place reduced (p=0.02) shrub cover in comparison to the untrenched controls at the Parkland site (Table 6-3). This reduction may have been due to severing shrub roots extending out from the subplots by the trenching treatment. At the Boreal site a trenching

- canopy removal interaction ($p=0.03$) was observed in one year. Greater ($p<0.01$) shrub cover resulted from the trenched without a barrier plots in comparison to either trenched with a barrier or the untrenched control, when trenching was applied within the full aspen canopy plots. However, this increase was transient and not observed across canopy treatments, nor is there an apparent underlying ecological phenomenon for the differences. Hence, this effect may be spurious.

The forb plant group encompassed a wide range of species, and individual dynamics were highly variable and sometimes localized (Appendix 3). Overall, the only significant ($p<0.10$) cover response collectively among the forbs was an increase ($p<0.01$) at the Boreal site during 2002 with complete canopy removal (Table 6-3). Forbs also initially trended towards greater cover at the Parkland site with canopy removal, however cover declined in 2002, possibly as a consequence of the drought.

Similar to ANPP, graminoid cover showed the most substantial differences across sites and treatments (Table 6-3). Across years, graminoid cover was greater at the Parkland site ($p<0.0001$) and increased in response to canopy removal ($p<0.01$) and root trenching ($p<0.01$). No differences ($p<0.10$) in graminoid cover occurred at the Boreal site, although there was a trend of increasing cover with the combination of complete canopy removal and trenching with a barrier in place in comparison to the other treatment combinations (Table 6-3). At the Parkland site graminoid cover was greater in 2001 with no overstory than under either a partial ($p=0.05$) or full aspen canopy ($p<0.01$). Graminoid cover also responded positively to trenching in 2001 in plots with an aspen overstory, with greater cover after trenching with a barrier in place ($p=0.02$) than the untrenched control (Table 6-3). Treatment differences at the Parkland site were expressed through 2002, with greater cover once again with no overstory than under either a partial ($p=0.02$) or full aspen canopy ($p<0.01$). Trenching also influenced graminoid cover through 2002, although in that year it interacted with the level of aspen ($p=0.04$), and was only expressed within the partial canopy removal plots (Table 6-3).

The majority of graminoid and total understory cover increases at the Parkland site in 2002 were from increases in smooth bromegrass and Kentucky bluegrass (*Poa pratensis* L.). Both are introduced species that have become naturalized in the Parkland

and both are relatively drought tolerant. The muted response of graminoid cover to canopy and root trenching treatments at the Boreal site may reflect the lower initial cover of these species. Alternately, the predominantly native boreal grass species may be relatively less competitive, requiring full canopy removal and reduction of root interaction before increasing substantially. The latter theory seems less plausible however, given that the most common grass species at the Boreal site was marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.), which has been observed to be an aggressive competitor for soil resources (Landhäusser and Lieffers 1998, Chapters 3 and 4, this volume).

Total cover of ground layer vegetation (forbs, graminoids and low shrubs summed) also displayed differences in relation to aspen canopy cover ($p<0.01$) at the Parkland site, but not at the Boreal site. Although total plant cover was similar ($p=0.31$) at both sites, canopy removal increased total ground vegetation cover at the Parkland site in both 2001 ($p=0.03$) and 2002 ($p<0.0001$). Total ground layer vegetation cover was lower with a full canopy in 2001 than with partial ($p=0.02$) or full canopy removal ($p=0.02$), but no difference existed ($p=0.94$) between the latter two treatments. In 2002, total plant cover increased with increasing level of canopy removal and differed between all canopy treatments ($p<0.0001$). The difference in total plant cover at the Parkland site in both years was due almost entirely to marked changes in graminoid cover.

Aspen cover also had a predictable, but important effects on leaf litter cover (Figure 6-6). There were greater amounts of aspen leaf litter at the Boreal site ($p<0.01$), and leaf litter cover generally decreased with the level of canopy removal ($p<0.01$) at the Parkland site in both years. In contrast, and possibly due to slower decomposition rates, leaf litter cover at the Boreal site did not differ ($p=0.28$) among canopy treatments in the first year following treatment and did not differ ($p=0.32$) between the full and partial aspen canopy plots through 2002. Leaf litter may have played an important role in moisture conservation and accounted for some of the observed net increase in soil water under partial and full aspen canopies during the drought (see Chapter 5, this volume).

Understory Species Diversity

Species diversity, as measured by Shannon or Simpson's indices, or species density (Tables 6-4) did not differ (p>0.15) with canopy removal or root trenching treatments at the Boreal site over the course of the experiment. Plant communities at the Parkland site were less diverse (p<0.0001) than at the Boreal site, and also showed significant differences in relation to aspen canopy removal and root trenching in 2002. Both Shannon (p=0.02) and Simpson (p=0.03) indices declined at the Parkland site with complete overstory removal. Moreover, Shannon diversity was lower in the openings than those under either full (p=0.01) or partial (p=0.02) aspen canopies. Shannon diversity did not differ (p=0.59) however, in 2002 between the partial and full canopy treatments. These results were mirrored in the Simpson's index (p<0.05). In contrast, only root trenching within the full aspen canopy plots influenced (p=0.06) species density in 2002, and this result may be spurious. There was a slightly greater number of species (p=0.04) on plots trenched with a barrier than on those trenched without a barrier (Table 6-4).

Because species richness (as measured in species density) was stable between canopy treatments, the decline in Shannon and Simpson indices at the Parkland site in the openings can be attributed to a reduction in the evenness (relative dominance) of the species. Indeed, the lower diversity measures at the Parkland site corresponded to increases in the cover of two prominent grass species (smooth bromegrass and Kentucky bluegrass). Declines in understory diversity therefore were linked to favourable growing conditions for these grass dominants coupled with a decline in forb species cover at the Parkland site in 2002.

A complex cross-over interaction in 2002 of canopy removal and root trenching without barrier was evident in Simpson (p=0.01) diversity. The same trend (with less significance) was also observed in Shannon diversity (p=0.07) and species density (p=0.08). At both sites, trenching without a barrier resulted in greater diversity with partial or complete canopy removal in comparison to trenching with a barrier or the untrenched controls. In contrast, with full aspen cover the reverse results were observed; plots trenched without a barrier had lower diversity than the other trenching treatments.

The synchronistic changes of Simpson and Shannon indices with changes in species density, suggest the differences were due to relative increases or decreases in the number of species present (richness). This phenomenon may indicate the interplay of drought and aspen root regrowth into the trenched subplots, and requires further investigation.

Understory Dynamics and Resource Levels

Understory PAR levels had a strong influence on cover and ANPP of understory vegetation. Across years, sites and treatments, PAR availability alone explained 40% ($p<0.0001$) of ANPP variation and 11% ($p<0.0001$) of ground layer vegetation cover variability. Moreover, these relationships were stronger at the Parkland site; most of the variation ($r^2=0.53$, $p<0.0001$) in ANPP was attributable to PAR at the Parkland site, whereas a much weaker relationship was found at the Boreal site ($r^2=0.22$, $p<0.0001$). Ground layer vegetation cover also displayed a stronger relationship to PAR at the Parkland site ($r^2=0.32$, $p<0.0001$), but did not relate to total cover at the Boreal site ($p=0.37$).

Part of the site differences in total understory ANPP can be attributed to the response of graminoids and their relationship to PAR. While the correlations between forb and shrub ANPP to PAR were weak (both $r^2=0.06$, $p<0.0001$), the overall relationship of graminoid ANPP to PAR was more substantial ($r^2=0.26$, $p<0.0001$). Indeed, by 2002, most (73 to 89%) of the understory ANPP increase at the Parkland site with partial or full canopy removal resulted from increased graminoid production, of which a substantial portion is explained by its relationship to the average available PAR ($r^2=0.41$, $p<0.0001$). Similarly, graminoid cover was strongly related to PAR ($r^2=0.57$, $p<0.0001$) at the Parkland site. Graminoids also related significantly to PAR availability at the Boreal site, but the latter explained much less of the variability in both ANPP ($r^2=0.07$, $p<0.001$) and cover ($r^2=0.03$, $p=0.04$), and overall, grasses contributed much less to total ANPP in 2002 (0-19%). Substantial increases in grass production within the Boreal site (19 ± 7% of total ANPP) only developed with complete canopy removal and reduction of root competition with trenching and placement of a barrier. This once again suggests that Boreal grasses required a minimum threshold in available light, which was not met by the partial canopy treatment tested. Moreover, the predominantly native grass species at the Boreal site possibly were less able to compete for below-ground resources than the mostly introduced grass species at the Parkland site.

Regression of multiple environmental variables against ANPP in 2002 once again highlights the importance of PAR to Parkland grass species production, but also provides insight into the importance of soil moisture and N availability for all vegetation components. Total ANPP in 2002 related most strongly to PAR availability and early season soil moisture content (Table 6-5). Total ANPP also correlated negatively to NH_4-N levels in spring 2003 (see regression coefficients Table 6-5). As these levels represent the unused or previously immobile portion of soil N, the negative correlation likely reflects the fact that plots with more growth in 2002 would have drawn the soil N reserves lower, and does not reflect a negative effect of N on understory growth.

Within plant groups, forb ANPP only correlated to soil moisture availability throughout the 2002 growing season (Table 6-5). Shrub ANPP showed the weakest correlations to resource availability, with inclusion of mid-growing season soil moisture and NH_4-N levels in 2002 producing the best fit model (Table 6-5). In contrast, graminoid ANPP was the only component that related significantly to fractional PAR availability. Modeled across sites, PAR explained 15% of the graminoid ANPP and was of secondary importance to 2003 NH_4-N levels (Table 6-5). When examined on a site-by-site basis however, an important dichotomy develops which corroborates the graminoid ANPP response to canopy removal and root trenching treatments. At the Parkland site, PAR (partial $r^2=0.27$, $p<0.0001$) was positively correlated to graminoid ANPP, and explained the most variability in the ANPP model. Mid-May soil moisture (partial $r^2=0.11$, $p<0.01$) was negatively correlated to graminoid ANPP at the Parkland site, and NH_4-N levels did not ($p=0.09$) correlate to ANPP. In contrast, mid-May soil moisture (partial $r^2=0.11$, $p=0.01$) and spring 2003 NH_4-N levels (partial $r^2=0.08$, $p=0.03$) were the two most important variables contributing to Boreal site graminoid ANPP. Understory PAR completed the regression model for the Boreal site, but explained the least amount of variation (partial $r^2=0.07$, $p=0.04$) of the three significant variables. These site correlation patterns corroborate the treatment differences observed between sites. Graminoid production at the Parkland site increased sharply with aspen canopy removal and inconsistently with root trenching, matching the pattern of strong correlation to PAR and secondary importance of soil moisture and N. In contrast, significant graminoid production increases at the Boreal site resulted only from complete canopy removal (increasing PAR penetration) and root trenching with a barrier in place (limiting below-ground competition).

Conclusion and Management Implications

In contrast with the findings of Ellison and Houston (1958), above-ground effects had the strongest effect on aspen understory ANPP at the Parkland and Boreal sites examined. The greatest changes in understory ANPP were in response to canopy removal with less consistent significant changes resulting from reduction of root interactions. Soil resources were an important factor for understory production and cover development, particularly among forbs. When root trenching was significant, it generally occurred with concomitant increases in PAR resulting from reductions in the aspen canopy. This response was particularly strong among grass and grass-like species. Indeed, increases in graminoid cover in response to root trenching at the Parkland site only occurred with partial or full aspen canopy removal. Likewise, full overstory removal was required before root trenching produced positive changes in Boreal graminoid ANPP.

Understory production was greatest with complete overstory removal at the Boreal site, but a partial canopy at the Parkland site produced comparable understory biomass to that of complete canopy removal. Understory gains with a partial canopy may be attributed to favourable microclimatic conditions of a closed forest retained by the partial aspen cover, while simultaneously increasing PAR penetration. Openings at both sites experienced less favourable microclimatic conditions with a shorter frost-free period, greater incidence and severity of very high growing season temperatures, and more severe soil drying in the Parkland during drought (see Chapter 5, this volume). Consequently, the Parkland shows good agroforestry potential from the standpoint of aspen thinning leading to potential facilitation of understory production. In contrast, limited potential for facilitation at the Boreal site with partial overstory appeared to exist with the thinning treatment tested. Understory microclimate was of secondary importance to solar input because independent of root zone influences, understory ANPP at the Boreal site increased proportionately to the level of aspen removal. A wider range of tree densities between complete canopy removal and the partial canopy tested in this study need to be examined in the Boreal to determine if a favourable light availability threshold exists and can be met with a lower aspen density.

The marginal understory production increase between partial and complete canopy removal at the Parkland site must also be balanced against other considerations in determining the value of agroforestry systems. For example, the observed reductions in species diversity between partial and full canopies may factor into the land use decision making. Indeed, this may be an important and over-riding consideration in some management settings where maintaining species diversity and associated wildlife habitat is a desired or legally mandated condition of the land management prescription. Moreover, in agroforestry systems, tree cover can improve animal welfare by sheltering animals from climatic extremes. Shade or wind shelter from trees can reduce heat stress in animals during summer and protect from wind chill during winter, both of which are linked to improved animal production (Silanikove 2000). Aesthetics and economic diversification (from conventional forestry or agriculture) may also factor significantly in adopting an agroforestry system. Thus, other considerations may factor into adopting an agroforestry approach, and production potentials in the Parkland appear to make this possible without substantial sacrifices in total understory ANPP.

Shifts in understory species composition occurred in response to changes in resource availability, and create interesting possibilities for the further development of northern agroforestry systems. With further elucidation of the correct light thresholds it may be possible to achieve either increased herbage or shrub production, by reducing aspen canopies to the appropriate density and cover. This gives land managers the flexibility to structure their overstory to suit understory needs, or to choose between alternative agroforestry systems (silvopastoral systems versus multi-canopy layered forest farming) as the wood fibre and understory crop markets dictate.

Production patterns in 2002 suggest that independent of agroforestry opportunities, retaining tree cover in the Parkland may buffer the effects of a drought. This provides a strong rationale for maintaining the landscape diversity inherent to the Parkland for sustainable rangeland production where cyclical droughts are expected. Partial aspen canopies at both sites have the added advantages of greatly reducing aspen regeneration (suckering) in comparison to complete canopy removal, and in providing substantial leaf litter inputs. As a consequence silvopastoral systems could have an advantage over complete aspen removal for conventional pasture development. The strong suckering response of aspen and related poplars can necessitate retreatment within 4-5 years after clearing to maintain accessible forage production in the midst of dense aspen regeneration (Bailey and Wroe 1974). By providing longer-term, stable forage production with partial aspen retention, silvopastoral systems may have an economic advantage over complete clearing of aspen forests because although the production levels may be initially lower, levels may be retained longer without further inputs. Moreover, the level of aspen litter fall was not restrictive of understory growth, but can potentially contribute positively to nutrient cycling and soil moisture conservation.

This experiment focused on the understory response to manipulation of existing aspen stands, however agroforestry systems must consider both understory and overstory production. Assessment of the aspen growth response was tempered by the brief period of observations relative to aspens' full life cycle. Despite this narrow window of observation, tree growth data trends indicate better wood fibre production potential in Boreal agroforestry combinations than in the Parkland, where drought undoubtedly restricted tree development. Further development of agroforestry systems for north temperate regions of Canada requires testing of additional tree species suitable to the range of climatic conditions. Rapid-growing, drought-tolerant tree species currently under development, such as improved-yield poplar varieties (e.g. *Populus x. euroamericana* cv 'Walker'), may be more suitable for Parkland agroforestry.

Table 6-1 Effects of stand thinning on aspen (*Populus tremuloides* Michx.) growth from June 2000 to October 2002. Least squares means (adjusted standard error).

	Parkland		**Boreal**	
Aspen Growth	**Full Canopy**	**Partial Canopy**	**Full Canopy**	**Partial Canopy**
Basal Area Increment (m^2 ha^{-1})	0.40 (0.2)	0.13 (0.2)	0.64 (0.2)	0.48 (0.2)
Basal Area Growth per Tree (m^2 $stem^{-1}$)	0.03 (0.01)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)
Relative Diameter Growth (cm cm^{-1} initial diameter), RGR_D	0.09 (0.03)	0.10 (0.03)	0.10 (0.03)	0.14 (0.03)
Height Growth** (m)	0.72 (0.14)	0.90 (0.14)	0.44 (0.14)	1.43 (0.14)
Relative Height Growth* (m m^{-1} of initial height), RGR_H	0.10 (0.03)	0.14 (0.03)	0.16 (0.03)	0.24 (0.03)

* Canopy removal treatment significant ($p<0.05$)
** Canopy removal by site interaction ($p<0.05$)

Table 6-2 Aspen (*Populus tremuloides* Michx.) canopy and root zone effects on above-ground net primary production (kg ha^{-1}) of understory shrubs (< 1-m tall), forbs and graminoids. Values are the least squares means. Adjusted standard errors for shrub, forb and graminoid means are 99, 99, and 172 kg ha^{-1}, respectively.

	Aspen	Root	Shrubs			Forbs			Graminoids		
Site	**Canopy**	**Trenching**	**2000**	**2001**	**2002**	**2000**	**2001**	**2002**	**2000**	**2001**	**2002**
Parkland	Full	TB[1]	94	188	211	53	135	153	150	296	383
		TNB[2]	103	122	163	37	75	296	172	180	366
		UT[3]	88	114	199	68	57	119	146	188	549
	Partial	TB	101	216	171	99	84	86	371	1031	1556
		TNB	108	268	191	47	234	20	314	906	1838
		UT	157	248	112	55	49	17	228	774	1216
	None	TB	70	323	301	30	177	124	400	1322	1739
		TNB	124	256	317	54	340	387	274	990	1915
		UT	66	349	313	34	161	37	234	1204	1756
Boreal	Full	TB	151	230	300	230	246	369	35	37	48
		TNB	227	164	217	144	150	191	11	6	4
		UT	130	248	397	197	187	219	14	12	8
	Partial	TB	119	342	604	223	242	477	7	5	3
		TNB	140	342	747	286	242	235	26	17	156
		UT	114	341	775	239	356	340	11	43	34
	None	TB	176	432	1019	204	531	1364	31	110	574
		TNB	101	178	682	206	225	1391	5	12	101
		UT	157	227	589	282	323	1449	20	47	236

[1] Roots Trenched and a Plastic Barrier in Place. [2] Roots trenched without a barrier in place. [3] Untrenched.

Table 6-3 Aspen (*Populus tremuloides* Michx.) canopy and root zone effects on tall shrub (>1-m tall), low shrub (< 1-m tall), forb and graminoid canopy cover (%) from 2000 to 2002. Values are the least squares means. Adjusted standard errors for tall shrub (>1-m tall), low shrub, forb and graminoid cover values are 8.3, 9.5, 6.6 and 4.5%, respectively.

	Aspen	Root	Tall Shrubs			Low Shrubs			Forbs			Graminoids		
Site	**Canopy**	**Trenching**	**2000**	**2001**	**2002**	**2000**	**2001**	**2002**	**2000**	**2001**	**2002**	**2000**	**2001**	**2002**
Parkland	Full	TB[1]	5.0	2.5	10.0	16.9	20.6	25.0	15.2	14.8	10.3	11.2	14.7	19.6
		TNB[2]	5.8	10.0	10.8	22.2	20.5	23.0	7.3	9.0	7.3	8.0	3.6	18.2
		UT[3]	5.8	5.8	3.7	17.3	44.0	30.8	9.8	10.8	9.5	7.8	6.4	8.4
	Partial	TB	1.7	2.5	6.7	14.7	16.8	12.3	7.0	14.3	3.4	10.0	44.3	37.3
		TNB	9.5	5.3	8.3	22.3	16.4	24.8	12.0	22.4	3.8	8.7	28.4	34.9
		UT	8.7	5.0	5.3	19.7	23.0	22.7	8.3	11.0	4.1	5.3	18.5	14.8
	None	TB	0.3	0.0	0.0	16.8	23.8	17.1	11.7	27.3	6.2	11.6	46.3	79.4
		TNB	0.8	0.8	3.2	29.9	32.7	22.8	3.8	20.7	6.8	8.7	39.3	52.3
		UT	0.0	0.0	0.0	46.9	52.6	38.3	2.9	9.8	3.7	9.0	45.9	68.3
Boreal	Full	TB	22.5	17.5	14.3	22.5	19.9	24.1	20.6	27.3	44.6	0.7	0.7	1.3
		TNB	38.3	42.8	41.7	22.3	57.9	51.3	22.0	20.5	29.1	0.7	0.4	1.8
		UT	20.3	12.7	17.8	20.5	22.8	28.2	15.3	23.6	31.0	0.7	0.8	2.6
	Partial	TB	25.3	0.5	2.8	30.5	27.1	34.6	12.4	29.6	38.5	0.3	0.1	1.8
		TNB	44.2	2.5	8.5	27.0	18.8	35.4	15.2	20.9	37.2	0.3	0.1	0.7
		UT	43.7	6.7	8.3	24.3	23.1	39.8	14.3	31.5	33.3	0.1	2.8	0.3
	None	TB	36.2	3.3	8.3	32.4	37.4	48.4	19.4	16.3	61.6	0.5	1.1	8.6
		TNB	28.3	2.8	2.8	41.4	37.5	52.0	20.0	23.6	65.8	0.3	0.2	2.3
		UT	37.5	19.5	20.3	21.3	47.3	46.5	20.1	22.3	45.7	0.6	1.7	3.0

[1] Roots Trenched and a Plastic Barrier in Place. [2] Roots Trenched without a Barrier in Place. [3] Untrenched.

Table 6-4 Aspen (*Populus tremuloides* Michx.) canopy and root zone effects on Shannon and Simpson diversity indices and species density of understory vascular plants from 2000 to 2002. Values are the least squares means. Adjusted standard errors for Shannon, Simpson and species density means are 0.15, 0.7, and 1.18, respectively.

Site	Aspen Canopy	Root Trenching	Shannon Diversity 2000	Shannon Diversity 2001	Shannon Diversity 2002	Simpson Diversity 2000	Simpson Diversity 2001	Simpson Diversity 2002	Species Density 2000	Species Density 2001	Species Density 2002
Parkland	Full	TB[1]	1.38	1.81	1.58	3.41	4.36	4.00	7.33	10.50	7.67
		TNB[2]	1.36	1.62	1.36	3.34	4.25	3.31	5.50	7.67	5.50
		UT[3]	1.48	1.52	1.55	3.54	3.58	3.79	8.17	8.33	7.17
	Partial	TB	1.60	1.36	1.35	3.99	3.07	3.36	6.00	7.50	5.67
		TNB	1.47	1.59	1.51	3.79	4.11	3.76	5.67	8.50	6.83
		UT	1.29	1.41	1.38	2.94	3.49	3.30	6.17	6.33	4.67
	None	TB	1.24	1.25	0.75	3.15	2.80	1.65	7.67	8.50	6.50
		TNB	1.29	1.52	1.29	3.10	3.50	2.78	6.00	8.17	7.33
		UT	1.13	1.13	0.85	2.64	2.42	1.93	5.67	7.00	5.83
Boreal	Full	TB	1.97	1.99	2.29	5.40	5.28	8.12	11.50	12.17	13.50
		TNB	1.89	1.71	1.95	5.69	3.89	5.55	10.67	11.00	11.50
		UT	2.08	2.02	2.26	6.77	5.70	7.79	11.33	12.00	13.17
	Partial	TB	1.80	1.61	2.08	4.95	3.78	6.04	11.33	10.50	12.50
		TNB	1.88	1.58	2.07	5.34	3.82	6.12	9.83	9.33	14.17
		UT	1.68	1.67	1.89	4.16	4.09	4.81	11.83	12.17	13.50
	None	TB	1.98	1.82	2.07	6.06	5.16	6.29	8.50	9.50	12.17
		TNB	1.79	1.74	2.19	4.96	4.74	7.44	9.50	9.17	11.67
		UT	1.81	1.80	2.05	5.21	4.26	6.09	8.67	9.17	10.33

[1] Roots Trenched and a Plastic Barrier in Place. [2] Roots Trenched without a Barrier in Place. [3] Untrenched.

Table 6-5 Relationship of aspen understory above-ground net primary production (ANPP) across sites to the proportion of open sky photosynthetically active radiation (PAR) intercepted, soil moisture (SM) at five dates in 2002, and available ammonium (NH_4) in July 2002 and early spring 2003.

Dependent Variable	Adjusted R^2	Independent Variable	Partial R^2	Model R^2	B[#]	Prob >|T|*
Total ANPP	0.50	PAR	0.40	0.40	17.8	<0.01
		SM, mid-May	0.08	0.47	4.5	<0.01
		NH_4, 2003	0.04	0.52	-2.0	<0.01
Forb ANPP	0.62	SM, early June	0.53	0.53	26.8	<0.01
		SM, mid July	0.04	0.56	18.2	<0.01
		SM, mid-June	0.05	0.61	6.4	<0.01
		SM, early August	0.02	0.63	3.2	0.03
Grass ANPP	0.53	NH_4, 2003	0.38	0.38	65.2	<0.01
		PAR	0.15	0.53	32.5	<0.01
		SM, early August	0.02	0.55	4.6	0.03
Shrub ANPP	0.29	NH_4, 2002	0.22	0.22	12.8	<0.01
		SM, early August	0.04	0.26	8.7	0.02
		SM, early June	0.05	0.31	3.0	<0.01

[#] Regression coefficient.

* Probability of the T-test of whether inclusion of this variable improves the overall fit of the regression model.

Figure 6-1 Effects of canopy removal on aspen (*Populus tremuloides* Michx.) growth and stand characteristics from June 2000 to October 2002. Vertical lines represent the adjusted standard error of the least squares means.

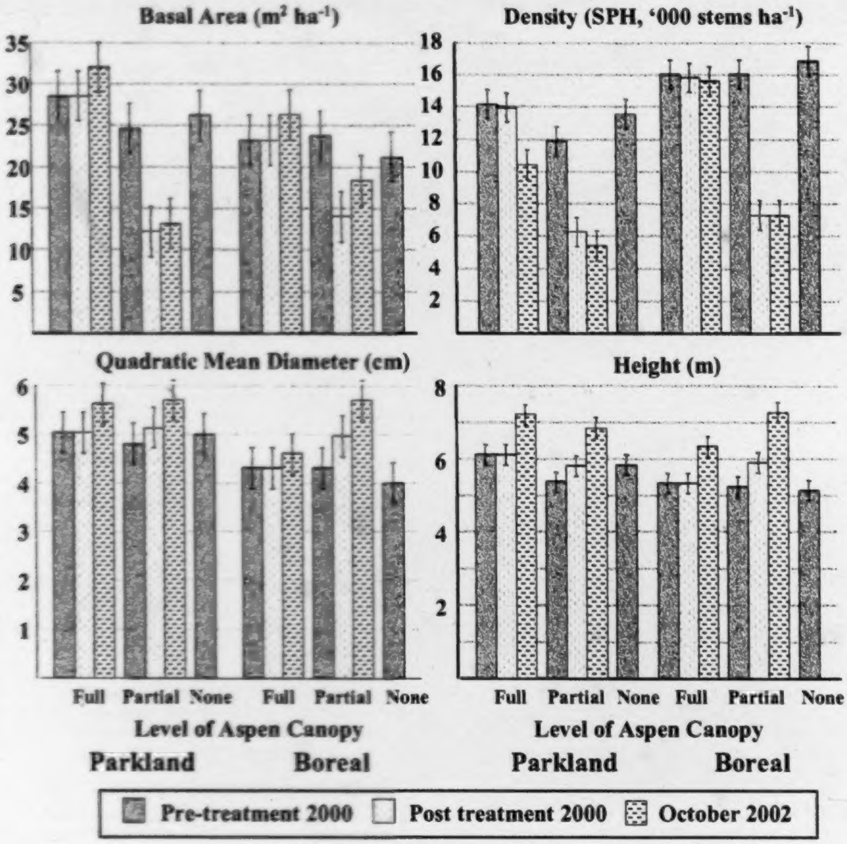


Figure 6-2 Relationship of aspen (*Populus tremuloides* Michx.) stand basal area and density to the proportion of open-sky photosynthetically active radiation (PAR) reaching the understory.

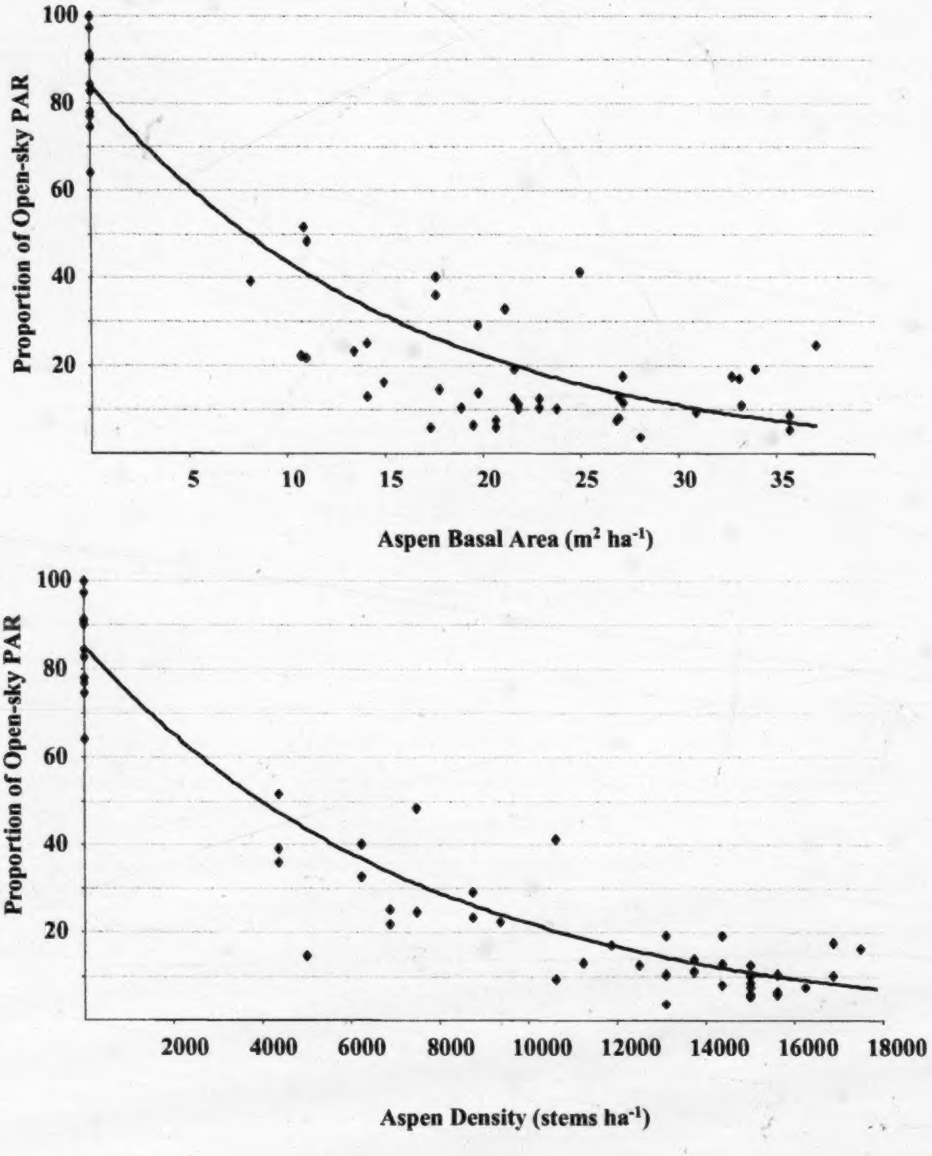


Figure 6-3 Effects of the level of aspen (*Populus tremuloides* Michx.) canopy on cumulative regeneration from April 2001 to October 2002. Vertical lines represent the adjusted standard error of the least squares means.

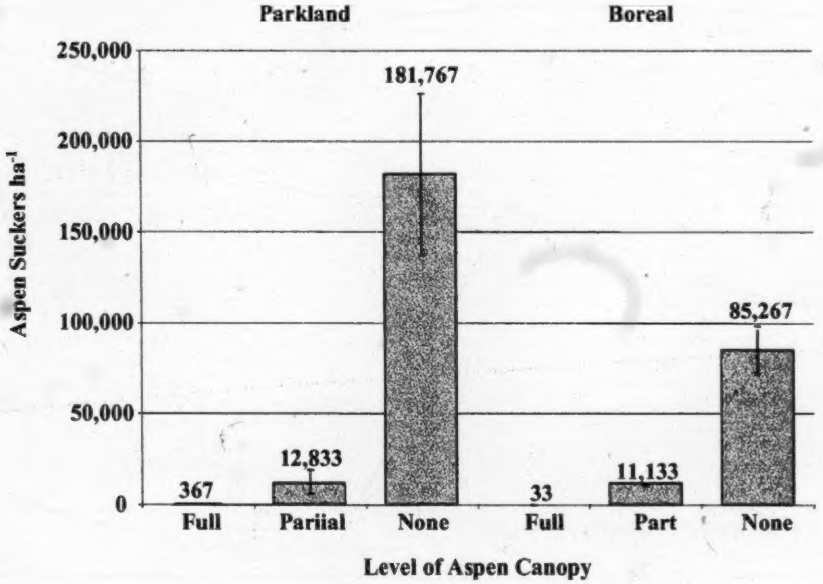


Figure 6-4 Aspen (*Populus tremuloides* Michx.) canopy and root zone effects on total understory above-ground net primary production at peak standing biomass from 2000 to 2002. Vertical lines represent the standard error of the least squares means.

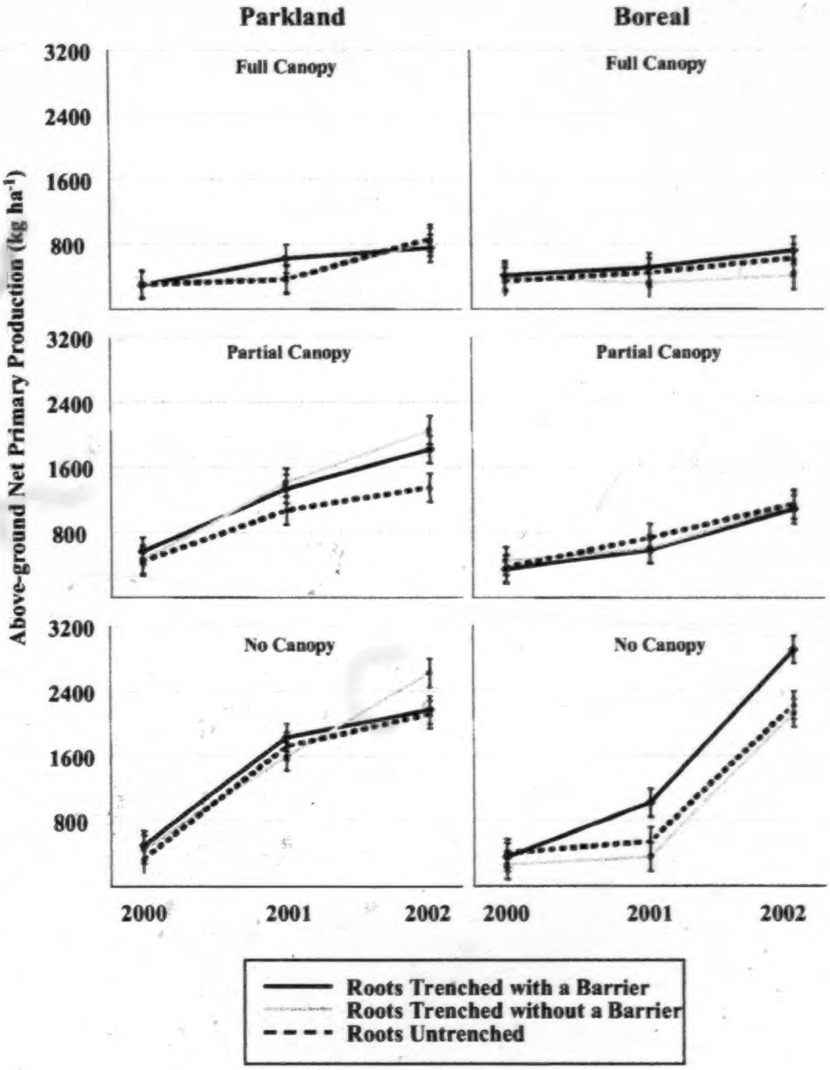


Figure 6-5 Aspen (*Populus tremuloides* Michx.) canopy and root zone effects on changes in relative yield of the major understory plant groups at peak standing biomass from 2000 to 2002. TB - Roots trenched with a plastic barrier in place. TNB –Roots trenched without a barrier. UT – Roots untrenched.

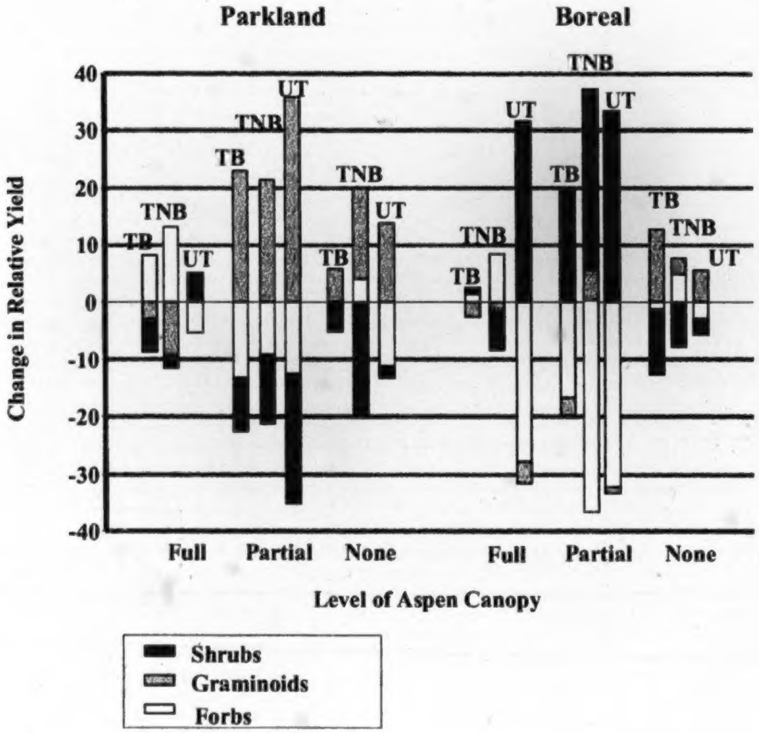
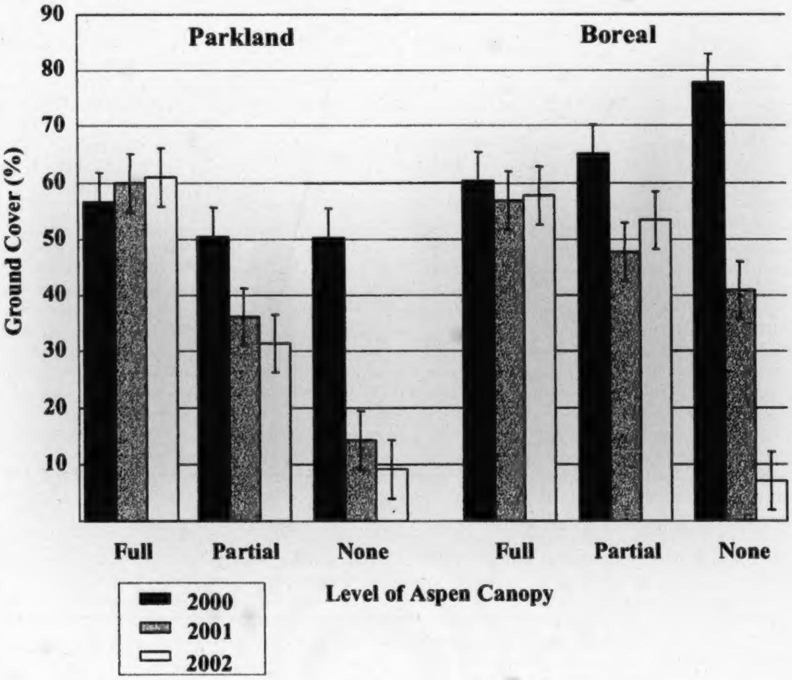


Figure 6-6 Effect of the level of aspen (*Populus tremuloides* Michx.) canopy on aspen leaf litter cover from 2000 to 2002. Vertical lines represent the adjusted standard error of the least squares means.



6.5 Literature Cited

Bailey, A.W. and R.A. Wroe. 1974. Aspen invasion in a portion of the Alberta Parklands. Journal of Range Management 27: 263-266.

Bartos, D.L. and W.F. Mueggler. 1982. Early succession following clearcutting of aspen communities in Northern Utah. Journal of Range Management 35: 764-768.

Belsky, A.J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients and tree-grass competition. Ecology 75: 922-932.

Bertness, M.D. and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9: 191-193.

Brooker, R.W. and T.V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos 81: 196-207.

Callaway, R.M. and L.R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958-1965.

Chipman, S.A. and E.A. Johnson. 2002. Understory vascular plant species diversity in the mixedwood boreal forest of western Canada. Ecological Applications 12: 588-601.

Comeau, P.G. 2001. Relationships between stand parameters and understory light in boreal aspen stands. British Columbia Journal of Ecosystems and Management 1(2): 8 p.

Coomes, D.A. and P.J. Grubb. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs 70(2): 171-207.

Daubenmire, R. 1959. A canopy coverage method of vegetational analysis. Northwest Science 33: 43-61.

Davis, M.A., K.J. Wrage and P.B. Reich. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. Journal of Ecology 86: 652-661.

Ellison, L. and W.R. Houston. 1958. Production of herbaceous vegetation in openings and under canopies of western aspen. Ecology 39: 337-345.

Grime, J. 1979. Plant Strategies and Vegetation Processes. John Wiley, New York.

Hilton, J.E. and A.W. Bailey. 1974. Forage production and utilization in a sprayed forest in Alberta. Journal of Range Management 27: 375-380.

Holmgren, M., M. Scheffer and M.A. Huston. 1997. The interplay of facilitation and competition in plant communities. Ecology 78: 1966-1975.

Hurlbert, S.H. 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52:577-586.

Kho, R.M. 2000. A general tree-environment-crop interaction equation for predictive understanding of agroforestry systems. Agriculture, Ecosystems and Environment 80: 87-100.

Landhäusser, S.M. and V.J. Lieffers. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis canadensis*. Canadian Journal of Forest Research 28:396-401.

Littell, R.C., W.W. Stroup and R.J. Freund. 2002. SAS® for Linear Models, Fourth Edition. SAS Institute Inc., Cary, NC, 466 p.

Olofsson, J., J. Moen and L. Oksanen. 1999. On the balance between positive and negative interactions in harsh environments. Oikos 86: 539-543.

Magurran, A.E. 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, New Jersey, 179 p.

McClaran, M.P. and J.W. Bartolome. 1989. Effect of *Quercus douglasii* (Fagaceae) on herbaceous understory along a rainfall gradient. Madrono 36: 141-153.

Messier, C.S., S. Parent and Y. Bergeron. 1998. Effects of overstory and understory vegetation on understory light environment in mixed boreal forests. Journal of Vegetation Science 9: 511-520.

Mueggler, W.F. and D.L. Bartos. 1977. Grindstone Flat and Big Flat exclosures - a 41-yr record of changes in clearcut aspen communities. Research Paper INT-195, USDA, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, UT, 16 p.

Paulsen, H.A. Jr. 1969. Forage values on a mountain grassland aspen range in Western Colorado. Journal of Range Management 22: 102-107.

Peterson, E.B. and N.M. Peterson. 1992. Ecology, management, and use of aspen and balsam poplar in the Prairie Provinces, Canada. Special Report 1, Forestry Canada, Northwest Region, Northern Forestry Centre, Edmonton, AB, 110 p.

Ratcliff, R.D., D.A. Duncan and S.E. Westfall. 1991. California oak-woodland overstory species affect herbage understory: Management implications. Journal of Range Management 44: 306-310.

Silanikove, N. 2000. Effects of heat stress on the welfare of extensively managed domestic ruminants. Livestock Production Science 67: 1-18.

Strong, W.L. and K.R. Leggat. 1992. Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife, Edmonton, AB, 59 p.

Strong, W.L. and G.H. La Roi. 1983. Rooting depth and successional development of selected boreal forest communities. Canadian Journal of Forest Research 13: 577-588.

Taylor, D.R., L.W. Aarssen and C. Loehle. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat template for plant life history strategies. Oikos 58: 239-250.

Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, NJ,

Wilson, J.B. 1988. Shoot competition and root competition. Journal of Applied Ecology 25: 279-296.

CHAPTER 7

Effects of a Simulated Aspen Understory Microclimate on Alfalfa Growth

7.1 Introduction

Optimal production in agroforestry systems requires an understanding of how plant-to-plant interactions influence the growth and yield of both tree and understory components. Plant growth under aspen (*Populus tremuloides* Michx.) is strongly influenced by the microclimate created by the forest overstory. Free-growing trees, because of their size and superior canopy position, dominate the use of incident light and create a physical barrier restricting air movement. These conditions, in turn, reduce photosynthetically active radiation (PAR) and temperature (T), and increase relative humidity (RH) in the understory. The resulting microclimate can produce a mixture of competitive and facilitative effects for understory plant growth (Callaway and Walker 1997). Reductions in the level of PAR to below optimal for photosynthesis can restrict growth. Modifications to T, airflow and RH however, can potentially benefit plants exclusively utilizing the Calvin cycle for photosynthesis (C3 plants) by decreasing the leaf-to-atmosphere vapour pressure difference (D).

The benefit of lowered D to C3 plants, and to a lesser extent in 'C4' plants, is conveyed through the influence on stomatal conductance. Stomatal conductance is important for water and nutrient acquisition, and is also necessary in C3 plants to exchange gases for active photosynthesis. As a result, photosynthesis in C3 plants is proportional to transpiration (Jones 1992), with the latter influenced by light intensity, D, T, wind, as well as plant and soil water status (Black and Kelliher 1989). Stomatal resistance to transpiration is the primary mechanism controlling water use in C3 plants with stomatal conductance generally decreasing linearly with increasing D as a result (Black and Kelliher 1989). A large D creates a strong gradient for the movement of water from a plant to the atmosphere, which unchecked would result in desiccation or xylem cavitation. To conserve water, a large D initiates stomatal closure in plants to slow or stop transpiration. This process simultaneously restricts or suspends gas exchange and photosynthesis (Dang *et al.* 1997), even when other conditions (PAR, soil moisture and nutrient levels) are optimal for plant growth. Recurring D-induced suspension of photosynthesis can ultimately reduce total annual production.

Alfalfa (*Medicago sativa* L.) is one of the most widely grown forage crops in the world and has potential for agroforestry applications (Lin *et al.* 2001). Alfalfa has well-adapted varieties for northern growing conditions but is generally intolerant of extensive shading (Wolf and Blaser 1972). Alfalfa also exhibits what is commonly referred to as "summer slump" whereby midsummer growth rates decline in comparison to early or late-season production. Although slowed summer growth has been attributed to elevated T (Al-Hamdani and Todd 1990), the concurrent effects of T and RH on D have not been explored. As with most C3 species, stomatal conductance in alfalfa is positively correlated to production (Forde *et al.* 1977). Indeed, reduced stomatal conductance was responsible for 50% of the overall decline in net photosynthesis of drought-stressed alfalfa (Nicolodi *et al.* 1988). Indirect evidence suggests increasing D has negative consequences for alfalfa growth and survival. For example, alfalfa exhibits sun-avoiding movement of its leaflets under conditions of increasing atmospheric vapour pressure deficit (Reed and Travis 1987), potentially as a mechanism to reduce leaf T and the associated D. Surprisingly, the limited research to date directly examining the effects of RH on alfalfa growth reported a negative relationship. Transpiration by alfalfa within sealed growth chambers decreased by 26-35% when RH increased by 10-20%, and this resulted in a 23 to 38% decrease in alfalfa dry matter accumulation (Radeva 1978).

Symbiotic associations of alfalfa and nitrogen (N) - fixing bacteria (*Rhizobium meliloti*), are capable of fixing greater than 150 kg N ha^{-1} yr^{-1} under good growing conditions (Walton 1983). While nodulation is positively related to light intensity (Chamblee 1972), the effects of RH and the interaction of PAR and RH on the N-fixing ability of alfalfa are not known.

The balance between potential facilitative and competitive above-ground effects of an aspen canopy on understory plant growth are unknown. If better understood, an optimal level of aspen cover could be prescribed for agroforestry applications that balance the negative effects of PAR reductions with the potential facilitation of understory growth through lower D.

7.2 Objectives and Hypotheses Tested

The general objective of this research was to isolate and compare the effects of variable PAR levels from the potentially facilitative effects of increased humidity (resulting in a lower D) resulting from an aspen overstory on the early growth and development of alfalfa. Controlled-environment growth chambers were used to simulate contrasting high and low levels of PAR and RH found under boreal aspen canopies in central Alberta, Canada. The following null hypotheses were tested:

1. Alfalfa growth does not vary with the levels of PAR corresponding to common mid-summer, midday values under partial and full boreal aspen canopies;
2. Alfalfa growth does not vary with the levels of RH corresponding to common mid-summer, midday values under partial and full boreal aspen canopies; and,
3. PAR and RH do not interact to influence alfalfa growth.

7.3 Methods

Alfalfa Establishment

Alfalfa (cv Nordica) was grown from seed in a sterilized, commercial soil mixture in 13 cm pots. Approximately 25 to 30 seeds, inoculated with *Rhizobium meliloti* bacteria, were broadcast onto the soil surface of each pot, covered with a shallow layer of soil and then watered to saturation. Pots were placed in controlled-environment growth chambers (16-hr photoperiod, 20 °C day/20 °C night T, 240 μmol m^{-2} s^{-1} PAR) and were watered daily to maintain adequate soil moisture for germination. Germination was rapid and seedlings were thinned to a density of 4 or 5 evenly-spaced plants per pot, 3 to 5 d after sowing. When seedlings had established true leaves (5 to 7 d later) the alfalfa was thinned to a density of 1 plant per pot. Subsets of these plants, chosen for uniformity of size, were then randomly assigned to the experimental units. At the commencement of light and humidity treatments, soil surfaces were covered with a 2-cm deep layer of finely-crushed rock to minimize evaporation differences between the contrasting humidity treatments (after Marsden *et al.* 1996).

Growth Chambers

Treatments were applied in controlled-environment growth chambers (Conviron™ CMP 4030). To simulate midsummer boreal conditions, the growth chambers were set with a 16-hour photoperiod, with day and night T of 22 and 17 °C, respectively. Day T was within the optimum range for alfalfa photosynthesis (Brown *et al.* 1972). Other environmental parameters were varied as per the treatment applications that follow:

1. RH: 75 and 40 %; and,
2. PAR: 240 and 75 µmol m^{-2} s^{-1}.

RH and PAR levels approximated values observed previously (see Chapter 5, this volume) under boreal aspen canopies at mid-summer with midday T of 20-25 °C.

Treatments were assigned to growth chambers in a split-plot design with a factorial arrangement of subplots. Each humidity treatment was randomly assigned to a separate growth chamber (main plot) and was applied with the growth chambers' internal humidifiers. Within growth chambers, partitions constructed from white plastic tubing were arranged to separate the area into two equally-sized compartments. A wood-framed centre divider covered in two layers of black landscape fabric was placed to block lateral light transmission between compartments. PAR treatments were randomly assigned to these chamber compartments (subplots) and were applied by using either filtered or unfiltered light. Unfiltered light (high PAR treatment) emanated from a combination of florescent and incandescent bulbs suspended from movable ballasts. Filtered light (low PAR treatment) was applied by placing a frame covered with a combination of charcoal-coloured fibreglass screening (New York Wire Co.) and acetate film bonded with a translucent layer of silver (3M Scotchtint Plus™ All Season Low E Window Film, LE50AMARL) on top of the chamber partitions, 60-cm above the pots. The film selectively filters red (R) wavelengths (655-665 nm) and simulates the effects of boreal aspen canopies removing more R than far-red (FR) wavelengths (725-735 nm), resulting in a decreased R:FR ratio (Ross *et al.* 1986).

During a test run of the experiment, T (to the nearest 0.01 °C) and RH (to the nearest 0.1 %) within each chamber compartment were recorded at 1-minute intervals with data loggers (Onset Computer Corporation, HOBO H8 Pro RH/Temp™). Growth chamber environmental controls were calibrated to these actual measures by trial-and-error. Maximum daily variations of up to 1.5 % RH and 1.4 °C from prescribed treatment levels were observed. Continuous forced air circulation provided for relatively homogeneous environmental conditions throughout the chamber. However, due to the heat load within the chambers emanating from the lights, an unavoidable 1.1 °C difference in day T was noted between the filtered and unfiltered compartments. No difference in night T was observed.

Levels of PAR (radiation in the 400 to 700 nm bands) were confirmed with a LICOR, LI-190SA™ quantum sensor placed in the centre of each empty chamber compartment, 13-cm above the chamber floor at a height corresponding to the top of the pots. PAR levels were monitored twice weekly, and were recalibrated to the treatment specifications as necessary by raising or lowering the light arrays and replacing older bulbs with newer units. Over five runs of the experiment (the test run and four experimental runs), high and low PAR levels averaged 240.5 ± 2.3 and 75.2 ± 0.8 μmol m^{-2} s^{-1}, respectively.

In each run, 25 pots (subsamples) were placed in each chamber compartment in an equidistant 5 by 5 arrangement. Pot locations within each treatment combination were initially determined randomly and were re-randomized weekly when the chambers were emptied for PAR calibrations. Re-randomization minimized the potentially confounding effects of location differences within the chambers. Pots were watered every 3 to 4 d to field capacity and were fertilized weekly with a dilute solution of 20-20-20 N P K water soluble fertilizer (0.8 g of fertilizer applied to each plant at each fertilization). Treatments were applied for 30 d, and the termination of each run coincided closely with early-bud stage of alfalfa development in the high PAR treatment.

Measures

Daytime leaf T was measured (to the nearest 0.1 °C) with an infra-red thermometer (0.2 °C resolution ± 1% of reading) on upper canopy alfalfa leaflets. Thermometers were held 1-cm from the surface, perpendicular to the leaf. These measures required opening the growth chamber doors, which initiated air T changes in the chamber. For this reason, measurements were made in rapid succession, with the total elapsed time required for measuring plants within a given compartment requiring less than 30 seconds. Measures were conducted on 2 sets of 10 plants within each treatment combination of one experimental run. There was 1 hr lapse between measures on plants within a given chamber to allow the internal air T to fully stabilize. Alfalfa D was calculated from leaf T, prescribed air T and RH, corrected for the conversion of the saturated pressure of pure water vapour to the saturation partial pressure of water vapour in moist air (Appendix 4, Jones 1992).

At the commencement of treatments and weekly thereafter, the number of leaves and shoot height (to the nearest 0.1 cm on the tallest stem) were recorded for each plant. Relative height growth (RGR_H) was determined for each weekly period by dividing the change in height from beginning to end of each period, by the height at the beginning period. At the termination of each 30 d experimental run, plants were harvested and separated at the root crown into above- and below-ground components. Leaves (including the petioles) were separated from the stems, and leaf area was determined (to the nearest 0.01 cm^2) for each plant by direct measurement on a LICOR, LI-3100™ area meter. Area per leaf (APL) was estimated by dividing the total leaf area by the total number of leaves at harvest for each plant.

Roots were extracted from the soil in a three-phase process. First, fine soil particles were separated from the root mass by washing the pot contents with low-pressure through a 1.70-mm Canadian Standard Sieve (10-mesh Tyler equivalent, No. 12 U.S. equivalent). The remaining sieve contents were floated in a container of clean water and extraneous material (including wood, vermiculite, and coarse soil fragments) was discarded. The remaining material was strained from the water through a piece of black landscape fabric, with recovery of root segments by hand. The presence of root nodulation was noted by visual examination of each plant. The nodules on all plants were very small (<3 mm diameter) and some broke loose during the root extraction procedure, making an accurate count of the total number impossible. As a result, comparisons were only made on the presence or absence of nodulation on each plant.

Yield components (leaves, stem and roots) for each plant were determined by drying at 70°C to constant mass, and weighing to the nearest 0.01 g. Various indices of plant mass and size were calculated to examine the effects of PAR and RH on alfalfa growth form and potential changes in carbohydrate allocation. Specific leaf weight (SLW) was estimated by dividing the total leaf mass for each plant by its total leaf area. The leaf-to-stem ratio (LS) was calculated by dividing leaf mass by the stem mass for each plant. Stem mass-to-length ratio (SML) was calculated by dividing stem mass by the sum of the lengths of all stems on each plant. Finally, the shoot-to-root mass ratio (SR) for each plant was determined by dividing the sum of leaf and stem masses by their respective root mass.

Analyses

Environmental controls failed during one run of the experiment causing internal temperatures to briefly rise to 40 °C. Desiccation of the majority of alfalfa was noted in this chamber. As a result, data from this replicate (high humidity treatment, both high and low PAR) were not used in the analyses, leaving 4 replicate runs of the low humidity treatments and 3 runs of the high humidity treatments.

An analysis of variance of the treatment effects on leaf T, D, leaf area, APL, mass, SLW, SML, LS, SR and the proportion of alfalfa plants developing root nodules was conducted with mixed-models (Table A2-17, Appendix 2, Littell *et al.* 2002) for a split-plot design. RH and PAR treatments were assumed to have fixed effects, while the variation between each experimental run was assumed to introduce random effects. A Kenward-Roger correction was applied to the degrees of freedom to eliminate sample size bias. Comparisons of RH means within PAR levels were obtained from F-tests on the least-squares means partitioned ("sliced") from the main PAR effects (Littell *et al.* 2002).

The influences of RH and PAR on weekly measures of height, RGR_H, and leaf and stem numbers were analyzed using mixed-models for repeated measures (Table A2-18, Appendix 2, Littell *et al.* 2002). A Kenward-Roger correction was applied to the degrees of freedom. The covariance models used in the analyses were selected iteratively for each response variable by testing several structures and comparing their Schwarz's Bayesian information criterion. This criterion test is based on the maximum likelihood fit corrected for the number of parameters in the model, analogous to the adjusted R^2 employed in multiple regression analyses. For the analysis of leaf and stem numbers, first-order auto-regressive structures were employed. An auto-regressive covariance structure reflects the fact that observations on the same unit are more highly correlated to those taken close together in time than those measured further away in time. For the analysis of height and RGR_H data, first-order ante-dependence covariance structures were utilized. Ante-dependence models can be regarded as a general extension of the autoregressive model (Littell *et al.* 2002) with the covariance between observations taken at two points in time being the product of variances at both points and the correlation between the two sampling intervals. Simple effects in the interaction of PAR or RH at each weekly interval were obtained from F-tests on the least-squares means partitioned ("sliced") from the main analyses.

7.4 Results and Discussion

Leaf Temperature and Vapour Pressure Difference

Leaf T corresponded closely to air T ($p<0.01$) and did not vary between RH treatments ($p=0.14$, Table 7-1). Leaf T under the low PAR treatment showed a similar 1 ^{o}C lower value than under the high PAR treatment that was recorded in air T. The combination of different compartment T and chamber RH significantly affected D ($p<0.01$) in the four treatment combinations (Table 7-1). Plants in the low RH treatments had more than double the D of those at the high RH levels. Air T differences corresponding to the PAR treatments also had a significant ($p=0.02$) influence on D, with high PAR treatments having approximately 6 % greater D than the corresponding low PAR treatments regardless of RH treatments.

Effects of PAR on Alfalfa Growth

Photosynthesis in well-watered alfalfa saturates between approximately 1200 and 1600 μmol m^{-2} s^{-1} (Antolín and Sánchez-Díaz 1993, Nicolodi *et al.* 1988). Thus, alfalfa growth is highly likely to positively respond to PAR increases between the lower (75 μmol m^{-2} s^{-1}) and upper (240 μmol m^{-2} s^{-1}) levels tested. Predictably therefore, PAR had a strong effect on alfalfa growth with a significant influence on the final height, leaf number, stem number, leaf area, SML, total mass and the mass of all individual yield components (all variables $p<0.01$, Figure 7-1, Table 7-1). Increasing PAR produced taller plants with greater stem mass. Because it also resulted in a greater SML, this suggests that the additional stem mass is accounted for in part by an increase in the thickness and/or density of stem tissue in the high PAR treatment. This difference may also have been compounded by etiolated stem growth in response to decreased R:FR light ratio at the lower PAR treatment. Etiolation would have resulted in taller stems of lower mass. The high PAR treatment also resulted in greater leaf numbers (Figure 7-1) and leaf mass (Table 7-1), but did not affect APL ($p=0.49$) or SLW ($p=0.48$), although there was a trend towards increasing SLW with decreasing PAR in both humidity treatments. PAR therefore, had a positive influence on leaf mass by increasing the total number of leaves per plant, and not by thickening or increasing the size of individual leaves. These data contradict the findings of Wolf and Blaser (1972) who found that below a threshold of 70% of full daylight (level of PAR not reported), alfalfa SLW decreased with declining light availability. PAR also did not influence the LS ($p=0.81$) or SR ($p=0.64$, Table 7-1), although SR trended towards an increase in the proportion of shoot mass at higher levels of PAR and RH. Lin *et al.* (2001) reported a decline in LS of alfalfa with either 50 or 80% shading of sunlight (levels of PAR not reported) and indicated that this was an important metric for alfalfa forage quality, because leaves are higher in protein and lower in fibre than stems. Therefore, with the exception of increased stem mass, the positive influence of PAR on alfalfa growth in the present study was primarily by producing more alfalfa phytomers, rather than enlarging existing structures.

Although PAR had a significant positive influence on RGR_H over the full period of alfalfa growth ($p<0.01$), this was due largely to a strong influence ($p=0.01$) on growth rates between the second and third week after the commencement of treatments (Figure 7-2). This coincided with a period of major expansion in stem length, as well as stem and leaf number of all plants (Figure 7-1). Thus, high PAR appeared to accelerate growth during an important development period. There was also a difference in the temporal development of new stems observed between the two PAR treatments. Alfalfa in the high PAR treatment began expressing additional stems during the second and third weeks (Figure 7-1). In contrast, alfalfa at the low PAR level generally did not form many additional stems until past the third week from the onset of treatments.

The presence of alfalfa-*Rhizobium* nodulation did not differ with PAR level ($p=0.87$). Although nodulation can be completely inhibited at low light intensities (Chamblee 1972), this threshold was not a factor in this experiment because some nodulation occurred in every treatment combination.

Effects of RH on Alfalfa Growth

The effects of RH on alfalfa growth were less pronounced, although still significant to several growth parameters. Alfalfa grown at the higher RH level had greater total leaf area ($p=0.05$), stem mass ($p=0.03$), shoot mass ($p=0.04$), and height ($p=0.02$) relative to those grown at low RH (Figure 7-1, Table 7-1). Similar to PAR, elevated RH increased stem length and stem mass. Likewise, the increase in leaf area was attributable to increased leaf numbers, not an increase in APL ($p=0.63$) (Table 7-1). However, unlike the response to PAR, SML did not increase, indicating the additional stem mass was due primarily to lengthening of the stem, and not through thickening or increased tissue density. Humidity also showed strong temporal variation in its effects on height, with no effects during the first 2 weeks of growth, but differences in the third ($p=0.05$) and fourth ($p<0.01$) weeks (Figure 7-1). Likewise, elevated RH only had an influence on alfalfa leaf number ($p=0.03$) in the final week of development.

The presence of alfalfa-*Rhizobium* nodulation did not differ with RH level ($p=0.17$). However, there was a trend towards increasing presence of nodulation at the higher RH in both PAR treatments (Table 7-1), which may have been masked by rather large variation introduced by other factors affecting nodulation. If elevated RH does increase nodulation, this has the potential to create a positive feedback in agroforestry systems, with trees benefiting from the enhanced N-fixed into the system as root nodules break down and release N into the soil.

In general, the influence of RH in this study had consistent, positive effects on alfalfa growth but was only strongly expressed on variables that were also positively affected by PAR. This is consistent with the theory that the primary benefit of elevated RH is through enhancing photosynthetic gas exchange by lowering the D, which in turn, facilitates photosynthesis provided that PAR is available at adequate levels.

Combined Effects of PAR and RH

PAR and RH treatments interacted to influence several attributes of alfalfa growth. Alfalfa leaf area ($p=0.03$), leaf mass ($p=0.03$), stem mass ($p<0.01$), shoot mass ($p=0.02$) and total mass ($p=0.04$) increased with greater RH at the high PAR level, but did not differ ($p=0.55$ to 0.88) at the low PAR level (Table 7-1). Likewise, the combined effects of RH and PAR affected the number of alfalfa stems, which diverged strongly ($p<0.01$) from weeks 2 to 4 (Figure 7-1). Unlike the mass and leaf variables, the number of stems per plant showed inconsistent effects at the high PAR level, but was greater with elevated RH at low PAR. Interactions of light and humidity have also been observed in the growth of other species. For example, an interaction of solar input and humidity was demonstrated in bracken fern (*Pteridium aquilinum* L.) under a Scot's pine (*Pinus sylvestris* L.) overstory (Roberts *et al.* 1984). In that experiment stomatal conductance declined ($r = 0.416$, $p<0.01$) with increasing atmospheric vapour pressure deficit and high irradiance (50 to 100 W m^{-2}), but demonstrated no consistent relationship at low irradiance (0 to 50 W m^{-2}). The divergent response to RH at different PAR levels is again consistent with the theory that the primary effect of elevated RH on C3 plant growth is through enhancing photosynthetic gas exchange through a lower D. At the low PAR level, the magnitude of the RH effect would be minimal due to the lower potential for photosynthesis. Conversely, at the higher PAR level, greater photosynthetic activity is augmented by a larger positive effect of RH.

Significance to Annual Production and Agroforestry Design

These data demonstrate that sustained, elevated RH has a positive effect on some aspects of alfalfa growth at a D typical of summer conditions in north temperate and lower boreal ecosystems. However, growth effects through time were generally only expressed from the middle to the end of the 30-d time frame of this experiment. This may indicate that RH must remain elevated for a considerable length of time to produce measurable positive effects. It is also important to note however, that PAR tended to have its greatest effects on alfalfa growth from the second week onward, and therefore, the observed effects of RH may be confounded somewhat with the normal early development patterns of alfalfa, particularly if its primary mechanism for enhancing growth is through augmenting the effects of PAR.

Under actual field conditions, RH and T are highly dynamic and display strong diurnal variation as well as, daily and seasonal fluctuation with local atmospheric conditions and weather patterns (see Chapter 5, this volume). Boreal and sub-boreal climates are restrictive for plant growth in part, because of the brief annual growing season (Bonan and Shugart 1989). Therefore, within this short growth period, recurring interruptions to photosynthesis could have a strong effect on total annual production. However, the prevalence or restrictions of large D to plant growth is not well-documented in these ecosystems, and the limited information does not demonstrate a strong role of D in long-term production. Indeed, although reduced transpiration and photosynthesis of the boreal shrub, beaked hazelnut (*Corylus cornuta* Marsh.) were observed on sunny days with a high ambient D, daily variation in carbon assimilation was small and appeared to be governed more by solar input than D (Hogg *et al.* 2000).

The results of this study indicate that elevated RH under aspen can compensate for some of the lost growth potential due to the concomitant light reductions, but can not fully counteract the reduced photosynthetic potential of alfalfa at the two PAR levels tested. At PAR levels closer to light saturation of photosynthesis in alfalfa however, diminishing returns in growth from additional PAR increments may result in RH having a proportionately greater overall effect on growth. Further testing of RH and PAR interactions across a broader range of conditions is necessary to fully assess this potential. Thus, designing agroforestry systems solely to elevate RH levels in the understory will likely not compensate for reductions in PAR unless light levels are closer to the saturation level for a given understory species. The role of other growth promoting factors associated with an overstory such as reduction of evaporation from the soil or enhanced nutrient cycling may also contribute to a greater net facilitative effect within integrated tree-forage productions systems and also require testing.

Conclusion

This research supports the theory of facilitation of understory growth from an aspen overstory through its effects on increasing RH and reducing understory plant D. With microclimatic conditions common at midsummer under boreal aspen canopies, increased RH had a small but measurable, positive effect on alfalfa growth, particularly at the higher level of PAR. However, its primary effect appears to be through enhancing the general growth of alfalfa on structures that are also positively affected by PAR. This includes lengthening of the stem, and thereby increasing the stem and total shoot mass, and increasing the number of leaves, thereby increasing the total leaf area. Agroforestry systems incorporating C3 plants may benefit from the incidental increase in RH and lowering of D due to the presence of an overstory layer, particularly where growing conditions are subject to recurrent high air T and low ambient RH. Additional research is needed to characterize the occurrence and importance of D to understory plant growth in different environments. The effects of variable RH and D at PAR levels closer to light saturation of the understory species is also needed to better understand the overall importance of RH-mediated facilitation to annual yields.

Table 7-1 The effects of contrasting high and low relative humidity (RH) and photosynthetically active radiation (PAR) on leaf temperature, leaf-to-atmosphere vapour pressure difference, growth and dry matter production of alfalfa (*Medicago sativa* L.). Values listed are the least-squares means (adjusted standard error). Means in the same row followed by the same letter are not significantly different from each other ($p>0.05$).

	High PAR				Low PAR			
	High RH		Low RH		High RH		Low RH	
Leaf-to-atmosphere vapour pressure difference (kPa), D	0.74 (0.01)	c	1.68 (0.01)	a	0.70 (0.01)	d	1.59 (0.01)	b
Leaf temperature (^{o}C)	22.4 (0.1)	a	22.5 (0.1)	a	21.5 (0.1)	b	21.6 (0.1)	b
Leaf area per plant (cm^2)	268.0 (18.4)	a	206.8 (16.0)	b	75.6 (18.4)	c	60.8 (16.0)	c
Area per leaf (cm^2), APL	0.34 (0.06)	a	0.39 (0.05)	a	0.32 (0.06)	a	0.33 (0.05)	a
Leaf mass (g)	1.16 (0.06)	a	0.94 (0.06)	b	0.31 (0.06)	c	0.30 (0.06)	c
Stem mass (g)	1.42 (0.10)	a	1.00 (0.09)	b	0.34 (0.10)	c	0.29 (0.09)	c
Shoot mass (g)	2.59 (0.16)	a	1.95 (0.14)	b	0.65 (0.16)	c	0.59 (0.14)	c
Root mass (g)	0.67 (0.09)	a	0.61 (0.07)	a	0.20 (0.09)	b	0.19 (0.07)	b
Total mass (g)	3.24 (0.23)	a	2.53 (0.20)	b	0.84 (0.23)	c	0.78 (0.20)	c
Leaf-to-stem mass ratio, LS	1.07 (0.11)	a	0.97 (0.10)	a	0.94 (0.11)	a	1.05 (0.10)	a
Stem mass to length ratio (mg cm^{-1}), SML	24.7 (1.2)	a	21.5 (1.2)	a	9.7 (1.2)	b	10.2 (1.2)	b
Shoot-to-root mass ratio, SR	4.17 (0.66)	a	3.55 (0.57)	a	3.71 (0.66)	a	3.39 (0.57)	a
Specific leaf weight (mg/cm^2), SLW	4.56 (0.63)	a	4.97 (0.55)	a	4.76 (0.63)	a	5.63 (0.55)	a
Nodulation (%)	19.3 (8.9)	a	13.0 (8.2)	a	22.0 (8.9)	a	12.0 (8.2)	a

Figure 7-1 The effects of contrasting high and low photosynthetically active radiation (PAR) and relative humidity (RH) on alfalfa (*Medicago sativa* L.) height, leaf number and total stem number. Vertical lines indicate the standard error.

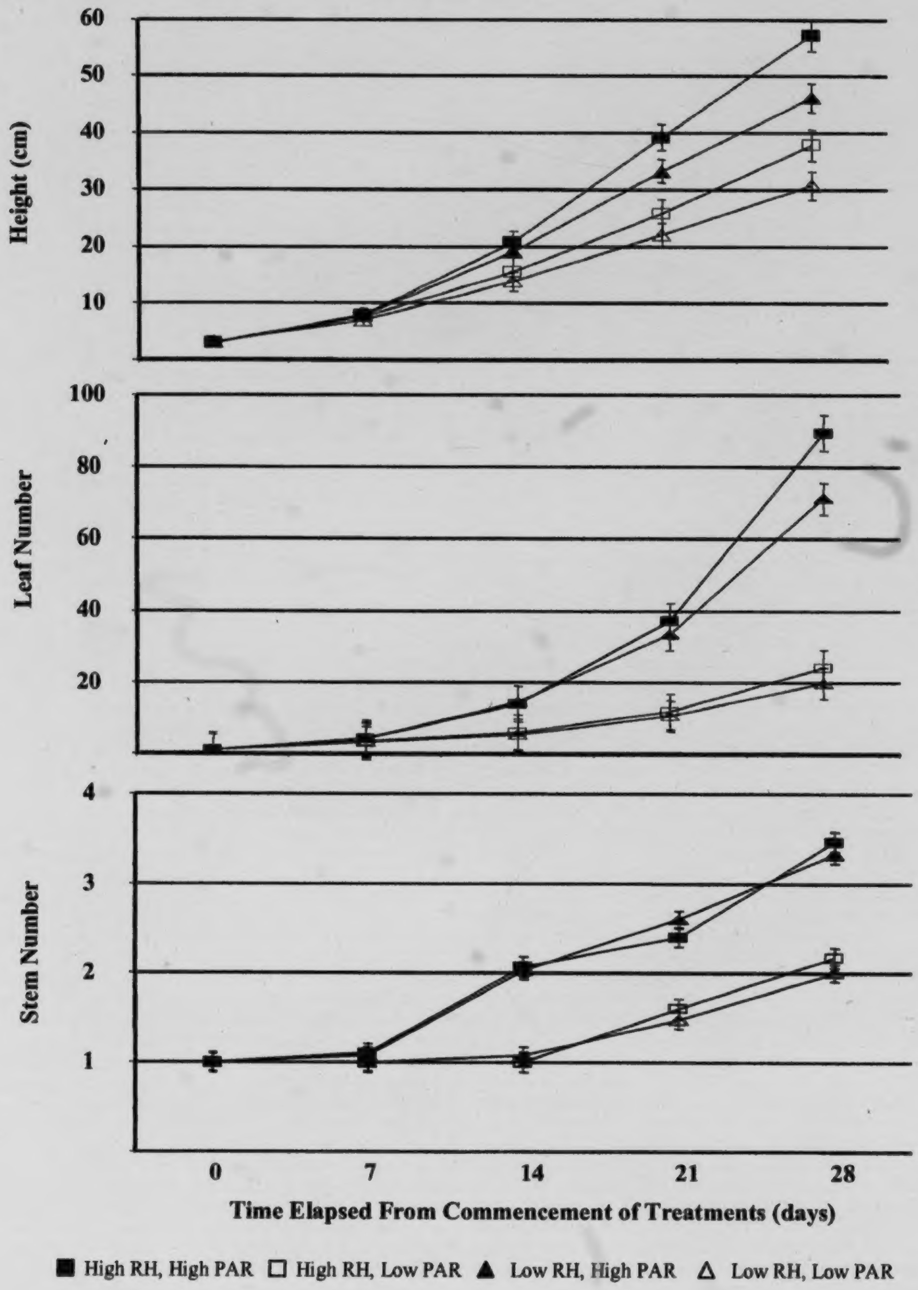
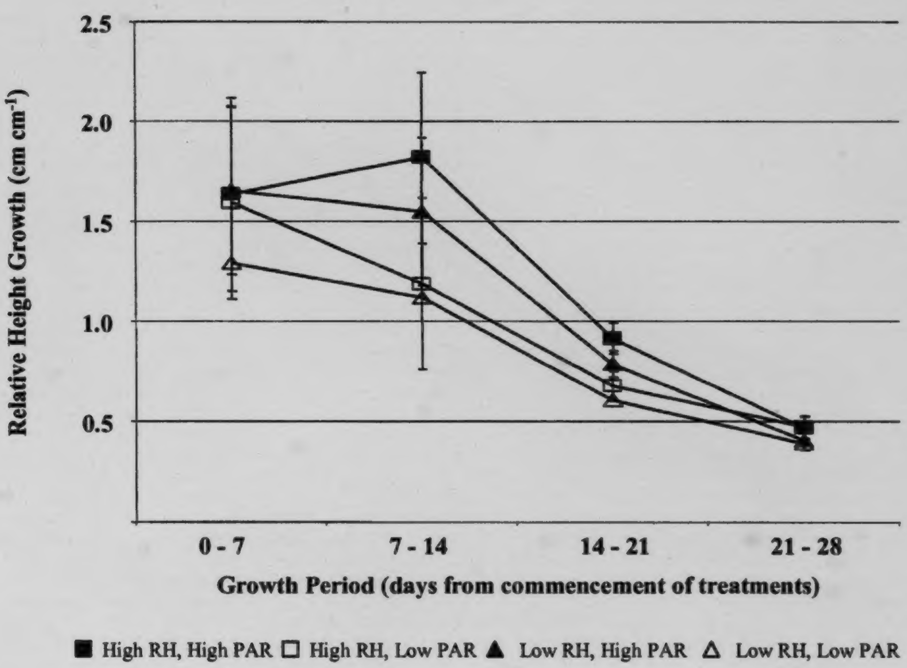


Figure 7-2 The effects of contrasting high and low photosynthetically active radiation (PAR) and relative humidity (RH) on relative height growth of alfalfa (*Medicago sativa* L.). Vertical lines indicate the standard error. Main effect of PAR was significant at $p<0.01$.



7.5 Literature Cited

Al-Hamdani, S. and G.W. Todd. 1990. Effect of temperature regimes on photosynthesis, respiration, and growth in alfalfa. Proceeding of the Oklahoma Academy of Science 70: 1-4.

Antolín, M.C. and M. Sánchez-Díaz. 1993. Effects of temporary droughts on photosynthesis of alfalfa plants. Journal of Experimental Botany 44: 1341-1349.

Black, T.A. and F.M. Kelliher. 1989. Processes controlling understory evapotranspiration. Philosophical Transactions of the Royal Society of London B 324: 207-231.

Bonan, G.B., and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. Annual Review of Ecological Systems 20: 1-28.

Brown, R.H., R.B. Pearce, D.D. Wolf and R.E. Blaser. 1972. Energy accumulation and utilization. Chapter 7, pp 143-166 *in*: Hansen, C.H. (editor). Alfalfa Science and Technology. Agronomy Number 15. American Society of Agronomy, Madison, WI, 812 p.

Callaway, R.M. and L.R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958-1965.

Chamblee, D.S. 1972. Relationships with other species in a mixture. Chapter 10, pp 211-228 *in*: Hansen, C.H. (editor). Alfalfa Science and Technology. Agronomy Number 15. American Society of Agronomy, Madison, WI, 812 p.

Dang, Q-L., H.A. Margolis, M.R. Coyea, M. Sy and G.J. Collatz. 1997. Regulation of branch level gas exchange of boreal trees: roles of shoot water potential and vapour pressure difference. Tree Physiology 17: 521-535.

Forde, B.J., K.J. Mitchell and E.A. Edge. 1977. Effect of temperature, vapour-pressure deficit and irradiance on transpiration rates of maize, paspalum, westerwolds, perennial ryegrass, peas, white clover and lucerne. Australian Journal of Plant Physiology 4: 889-899.

Hogg, E.H., B. Saugier, J-Y. Pontailler, T.A. Black, W. Chen, P.A. Hurdle and A. Wu. 2000. Responses of trembling aspen and hazelnut to vapour pressure deficit in boreal deciduous forest. Tree Physiology 20: 725-734.

Jones, H.G. 1992. Plants and microclimate, a quantitative approach to environmental plant physiology. 2nd Edition, Cambridge University Press, Cambridge, UK, 428 p.

Lin, C.H., R.L. McGraw, M.F. George and H.E. Garrett. 2001. Nutritive quality and morphological development under partial shade of some forage species with agroforestry potential. Agroforestry Systems 53: 269-281.

Littell, R.C., W.W. Stroup and R.J. Freund. 2002. SAS® for Linear Models, Fourth Edition. SAS Institute Inc., Cary, NC, 466 p.

Marsden, B.J., V.J. Lieffers and J.J. Zwiazek. 1996. The effect of humidity on photosynthesis and water relations of white spruce seedlings during the early establishment phase. Canadian Journal of Forest Research 26: 1015-1021.

Nicolodi, C., A. Massacci and G.D. Marco. 1988. Water status effects on net photosynthesis in field-grown alfalfa. Crop Science 28: 944-948.

Radeva, V. 1978. An enhanced air humidity influence on the lucerne plant transpiration. Rastenievud-Nauk 15: 27-34 (in Bulgarian, abstract in English).

Reed, R. and R.L. Travis. 1987. Paraheliotropic leaf movement in mature alfalfa canopies. Crop Science 27: 301-304.

Roberts, J., J.S. Wallace and R.M. Pitman. 1984. Factors affecting stomatal conductance of bracken below a forest canopy. Journal of Applied Ecology 21: 643-655.

Ross, M.S., L.B. Flanagan, and G.H. La Roi. 1986. Seasonal and successional changes in light quality and quantity in the understory of boreal forest ecosystems. Canadian Journal of Botany 64: 2792-2799.

Walton, P.D. 1983. Production and Management of Cultivated Forages. Reston Publishing Company, Inc., Reston, Virginia. p 240.

Wolf, D.D. and R.E. Blaser. 1972. Growth rate and physiology of alfalfa as influenced by canopy and light. Crop Science 12:23-26.

CHAPTER 8

Effects of Boreal Aspen on Alfalfa Leaf-to-Atmosphere Vapour Pressure Difference

8.1 Introduction

Optimal production in agroforestry systems requires an understanding of how plant-to-plant interactions influence the growth and yield of both tree and understory components. Plant growth under aspen (*Populus tremuloides* Michx.) is strongly influenced by the microclimate created by the forest overstory. Free-growing trees, because of their size and superior canopy position, dominate the use of incident light and create a physical barrier restricting air movement. These conditions, in turn, reduce photosynthetically active radiation (PAR) and temperature (T), and increase relative humidity (RH) in the understory. The resulting microclimate can produce a mixture of competitive and facilitative effects for understory plant growth. Reductions in PAR to levels below optimal for photosynthesis, restrict growth. Modifications to T, airflow and RH however, can potentially benefit plants that exclusively utilize the Calvin cycle for photosynthesis (C3 plants) by decreasing the leaf-to-atmosphere vapour pressure difference (D) (Jones 1992, Dang *et al.* 1997).

Alfalfa (*Medicago sativa* L.) is one of the most widely grown forage crops in the world and has potential for use in agroforestry applications (Lin *et al.* 2001). Indirect evidence suggests increasing D has negative consequences for alfalfa growth and survival. For example, alfalfa exhibits what is commonly referred to as "summer slump" whereby midsummer growth rates decline in comparison to early or late-season production. Although slowed summer growth has been attributed to elevated air T (Al-Hamdani and Todd 1990), the concurrent effects of T and RH on D have not been explored. Alfalfa also exhibits sun-avoiding movement of its leaflets under conditions of increasing atmospheric vapour pressure deficit (Reed and Travis 1987), potentially as a mechanism to reduce leaf T and thereby reduce D.

Transpiration and photosynthesis in boreal shrubs and trees are known to decrease with increasing D (Hogg *et al.* 2000), but this has not been recorded for alfalfa or other herbaceous species under field conditions. This study assessed alfalfa D under a range of different atmospheric conditions in the understory of boreal aspen stands.

8.2 Objectives and Hypotheses Tested

The objectives of this experiment were to determine how differing levels of boreal aspen canopy, under differing atmospheric field conditions, affect alfalfa leaf T and D. The following null hypotheses were tested:

1. Alfalfa leaf T does not vary with air T, RH or incident PAR under boreal aspen canopies; and,
2. Alfalfa D does not relate to air T, RH or incident PAR under boreal aspen canopies.

8.3 Methods

Research Site

This study was conducted at the Lakeland Agricultural Research Association lease southwest of Lac La Biche, Alberta (54° 33' N, 112° 05' W) in the Lower Boreal Mixedwood subregion (Strong and Leggat 1992). This area receives an average of 504 mm of precipitation annually with approximately half during the growing season (1970-2000 normal, Environment Canada). Research plots were located in a juvenile (20-yr old) aspen forest with an average density of 16,319 ± 367 stems ha^{-1}. Native shrubs and forbs, including low-bush cranberry (*Viburnum edule* (Michx.) Raf.), prickly rose (*Rosa acicularis* Lindl.) and wild sarsparilla (*Aralia nudicaulis* L.), dominated the understory. This experiment utilized canopy removal treatments from a concurrent study investigating the effects of aspen on understory microclimate and vegetation (Chapters 5 and 6, this volume). Nine, 10- x 10- m plots were randomly assigned to one of three aspen canopy removal treatments, each replicated three times, by cutting the appropriate number of aspen stems off at ground level in the fall of 2000:

1. no aspen canopy removal (control);
2. partial canopy removal (6,770 ± 640 stems ha^{-1}); and,
3. full aspen canopy removal.

Alfalfa Establishment

In each of 2001 and 2002, alfalfa (cv Nordica) was established from seed in 150- by 170-mm, black plastic pots containing an unsterilized, silt-loam field soil over a 5 cm base of gravel. Approximately 25 to 30 seeds, inoculated with a coating of *Rhizobium meliloti* bacteria, were broadcast onto the soil surface of each pot, covered with a shallow layer of soil and watered to soil saturation. Pots were placed outside with full sky exposure, but sheltered from the prevailing winds at the University of Alberta's Ellerslie Research Station, in Edmonton, AB (53° 25' N, 113° 33' W). Pots were watered regularly to maintain adequate soil moisture for germination and were weeded of other vegetation as necessary. After germination (approximately 10-14 d after seeding) the seedlings were thinned to a density of 4 or 5 evenly spaced plants per pot. When these seedlings had established true leaves (5 to 7 d later) the alfalfa was thinned again to a density of 1 plant per pot.

Three weeks after germination, a subset of these plants chosen for uniformity of size, were transported to the field research site; 16 plants were randomly assigned to each replicate of the aspen canopy removal treatments. Plants were watered at the time of transport, after which no artificial water was applied. Pots were grouped in an equidistant four by four spacing under 1-m^3 mesh-wire cages to protect them from disturbance and large animal herbivory. Vegetation under the cages taller than the surface of the pots was periodically removed as needed during the course of the experiment to isolate abiotic effects.

Measures

Direct measures of PAR (radiation in the 400 to 700 nm bands) were made with quantum sensors. In 2001, measures were taken with a Decagon AccuPAR™ ceptometer; in 2002, a LICOR, LI-190SA™ quantum sensor was used. In each year, 10 PAR measures per plot were taken above each grouping of pots, over a 1-hr period around solar noon and averaged. The relative amount of PAR intercepted by the aspen overstory was calculated by comparing the understory measures to readings in openings with an unobstructed sky view, taken within a few minutes of the subcanopy measures. Boundary layer air T (to the nearest 0.1 °C) and RH (to the nearest 0.1 %) were measured 50-cm above ground level in each plot. In 2001, measures were taken with an Oakton™ digital thermohygrometer; in 2002, T and RH were recorded at 5-minute intervals with data loggers (Onset Computer Corporation, HOBO H8 Pro RH/Temp™) located in the centre of each canopy removal plot. Volumetric soil moisture in each pot was recorded in 2002 at 3-week intervals with a Delta-T™ theta probe in both pots containing alfalfa, and pots with soil, but no vegetation.

Alfalfa leaf T was recorded periodically over both years with an infrared thermometer (0.2°C resolution ± 1% of reading) under a variety of contrasting atmospheric conditions (overcast or clear) and mid-day air T. Measures were conducted on days with uniform sky conditions and with very minimal (< 5 km hr^{-1}) or no wind. Leaf T was recorded on upper canopy alfalfa leaflets, with thermometers held 1-cm from the surface, perpendicular to the leaf. In 2001, timing of leaf T measures coincided with air T and RH measurements. In 2002, leaf T measures were matched to the closest record from the data loggers. Alfalfa D was calculated from leaf T, air T and RH, corrected for the conversion of the saturated pressure of pure water vapour to the saturation partial pressure of water vapour in moist air (Appendix 4, Jones 1992).

Alfalfa height, leaf number, damage and survival were recorded in both years at the commencement of the experiment and at 3-week intervals thereafter until harvest. Surviving plants were harvested to soil level for mass determination after having grown under the aspen canopy for 9 weeks. Plants were dried at 70 °C to constant mass and weighed to the nearest 0.1 g.

Analyses

High damage and mortality due to insect defoliation (2001) and an extended drought (2002) were observed and may have confounded some plant growth data. In some cases all subsamples within a given canopy replicate had either died or were completely defoliated. Data on plant height, leaf number and shoot mass therefore had either very low replication or strongly heterogeneous variances that could not be corrected with data transformation. Differences in alfalfa mortality and damage were tested with chi-square analyses of the counts between treatment groupings. Analyses of leaf T and D were conducted using mixed linear models for a completely random design (Littell *et al*. 2002). Canopy treatments were assumed to have fixed effects, while the variation between replicated canopy removal plots was assumed to introduce random effects (Table A2-19, Appendix 2). A Kenward-Roger correction was applied to the degrees of freedom to eliminate sample size bias.

Average alfalfa leaf T and D in each canopy treatment were regressed against levels of PAR, RH and boundary layer air T. Regressions of multiple independent variables were conducted using both forward stepwise and backward elimination techniques to find the combination and order of variables that produced the best-fit model. Plots of the residual values from the regression equations against their expected values indicated that linear models were appropriate for the analyses.

8.4 Results and Discussion

PAR and Soil Moisture

The proportion of open sky PAR alfalfa received varied consistently ($p<0.0001$) with the level of aspen canopy in all sampling periods of 2001 and 2002 (Table 8-1). Although the absolute level of PAR differed widely with cloud cover, the relative proportion between sampling periods was always greatest with complete canopy removal and least with full aspen canopy.

Soil moisture levels were not recorded in 2001. However, pots not under an aspen overstory were noticeably drier during some periods than those either under a full or partial overstory. Soil moisture in 2002 averaged 15.8 ± 0.2, 34.8 ± 0.3 and 23.4 ± 0.6% after 3, 6 and 9 weeks under the aspen canopy treatments, respectively, and did not differ among aspen canopy treatments ($p=0.13$ to 0.16), nor between pots containing alfalfa and those containing only soil ($p=0.23$ to 0.73). This uniformity might be due in part to the weather patterns experienced during 2002. A prolonged drought with negligible precipitation during the first month of the experiment (June) likely caused pots under all canopy treatments to dry to the extent that strong differences in overstory shading were masked by evaporation from pots. This was followed later in the growing season by two very heavy rainfalls. These large precipitation events made all pots uniformly wet, which again likely obscured any potential differences that may have arisen from differences in rainfall interception among the aspen canopy treatments.

Leaf Temperature and Vapour Pressure Difference

Leaf T varied with level of aspen canopy (p<0.02) under all sampling conditions except with uniform cloud cover and cool (11 °C) air T (p=0.59, Table 8-1). In each sampling period, leaf T was lowest under full aspen cover and trended towards increasing leaf T with decreasing aspen cover. This segregation was strongest with very hot (36 °C) air T, under cloudless sky. Under these conditions there was a significant (p<0.01) separation of leaf T between each canopy treatment. With hot (31 °C) or warm (20 °C) air T regimes, a full canopy also resulted in the lowest leaf T, however, differences between partial and complete canopy removal were inconsistent with a somewhat greater separation of leaf T differences under a clear sky at higher T. Across all sampling periods, air T, PAR and RH accounted for 97% (p<0.0001) of the variability in leaf T (Table 8-2). Boundary layer air T was responsible for 94% (p<0.0001) of the variability in leaf T and was the primary environmental factor influencing leaf T. Clawson *et al.* (1989) reported a similar strong relationship between alfalfa canopy T and air T. To a much smaller degree, the absolute level of PAR received (μmol m^{-2} s^{-1}) by the alfalfa also significantly (p<0.0001) contributed to leaf T differences, while RH had negligible effects (partial R^2=0.004, p=0.08).

The gradient in vapour pressures between plant and atmosphere is a function of leaf T, air T, and RH (Jones 1992). Indeed, these three variables accounted for almost all the variability (R^2=0.98, p<0.0001) in alfalfa D (Table 8-2) with leaf T having the largest influence (partial R^2=0.87, p<0.0001). Because of the dependence of leaf T on air T, however, there is strong colinearity between these two variables in their influence on alfalfa D. In fact, air T, PAR and RH accounted for 85% of the variability in alfalfa D with air T explaining most (partial R^2=0.68, p<0.0001) of the response (Table 8-2). As a consequence, alfalfa D displayed a similar pattern of response as leaf T to aspen canopy removal treatments (Figure 8-1). No difference ($p=0.93$) was observed in alfalfa D between canopy treatments under cloudy, cool conditions (11 °C). Without cloud cover there was a significant ($p<0.01$) decline in alfalfa D with increasing aspen canopy cover. This effect was most pronounced with very hot (36 °C) air T. Indeed, with these weather conditions and the absence of aspen cover, alfalfa D reached extreme values (maximum 7.7 kPa). Plants without an aspen overstory displayed substantial visible leaf damage and stem desiccation, and many died during the ensuing week after experiencing these extreme T and D.

Although the amount of PAR received by alfalfa had a small overall effect on alfalfa D over and above the influence of air T, these differences may have had a more significant role in the separation of aspen canopy effects, particularly under clear sky conditions where a high proportion of solar input was in the form of direct radiation. This can be seen in the effects of the amount of aspen canopy on the difference between leaf and air T (Figure 8-2). Under overcast skies all the light received is from diffuse radiation. With an overcast sky and cool air T, leaf T did not differ from air T ($p=0.11$ to 0.98). With these sky conditions and warmer air T, however, leaf T was slightly cooler than the air T ($p<0.01$), with the largest difference occurring without any aspen cover. Under clear sky conditions, when greater than 50% of the light is from direct solar input at mid-day, leaf T diverged sharply from air T, with a strong effect of the aspen canopy on both the magnitude and direction of the difference. Shading by the aspen overstory eliminated most of the direct beam radiation under a full aspen canopy and some of the direct insolation with a partial aspen cover. At hot air T (31 °C), alfalfa leaves were cooler ($p=0.06$) than the air under a partial or full aspen canopy, and warmer than the air ($p=0.06$) without an overstory (Figure 8-2). At very hot air T (36 °C), alfalfa leaves were again cooler than the air T ($p=0.03$) under a full aspen canopy and warmer than the air without aspen cover. However, with a partial aspen canopy, alfalfa leaf T did not ($p=0.95$) differ from air T under these climatic conditions.

In addition to the amount of direct beam radiation received by alfalfa leaves, D also influences the leaf-to-atmosphere T difference. A main cooling mechanism in plants is through the loss of latent heat carried in water vapour with the transpiration flow (Jones 1992). Because increasing D restricts or completely eliminates transpiration, this can create positive feedback resulting in elevated leaf T in the following manner. A large D triggers a decrease in transpiration, which in turn, elevates the leaf T and thus, increases D. Once transpiration is blocked, the only substantial heat-loss vector is through radiation from the plant across the surface boundary layer into the atmosphere. The difference between plant and air T together with laminar boundary layer resistance govern this process. Boundary layer resistance is a function of its thickness, which in turn, is largely a function of atmospheric turbulence (Jones 1992). Therefore, very hot, windless days can result in substantial heat damage to plants. Because leaf T sampling was conducted under nearly windless conditions (< 5 km hr^{-1}), direct radiation of heat from alfalfa would have been minimized. The maximum leaf T with very hot air T was 41.2 °C (Table 8-1). This T is within the range where McKenzie *et al.* (1988) suggest leaf protein and tissue degradation occurs in alfalfa.

Alfalfa Growth, Damage and Survival

The number of alfalfa leaves per plant was not affected by the aspen canopy treatments in 2001 (14 ± 1, $p=0.36$) or 2002 (17 ± 2, $p=0.54$). Likewise no differences were detected in alfalfa height at the end of the experimental period of 2001 (19.0 ± 1.3 cm, $p=0.37$) or 2002 (21.0 ± 1.9 cm, $p=0.71$). These data are likely confounded by the effects of variable insect damage however, and suffer from low statistical power and heteroscedasticity due to the low number of plants surviving to the end of the experiment in 2002.

Alfalfa mass was unaffected ($p=0.37$) by aspen canopy treatments in 2001, but similar to alfalfa height and leaf number, these data are likely confounded by the varying amounts of biomass removed by insect defoliation and variable mortality among the treatments. Alfalfa mass did differ ($p<0.01$) among canopy treatments in 2002. Alfalfa grown under a full aspen canopy (110 ± 176 mg) had less than 20% of the mass ($p=0.03$) of those grown without an aspen overstory (530 ± 44 mg). Alfalfa under a partial canopy (230 ± 76 mg) had less than half the mass of those without an aspen overstory ($p<0.01$), but did not differ ($p=0.54$) from the mass of plants under a full aspen canopy.

Insect damage to alfalfa leaves and stems was different among canopy treatments in 2001 (n=137, p<0.0001); plants under a partial canopy sustained less insect attack than those under either full or no canopy (Figure 8-3). Nearly all plants with either a full aspen canopy or no aspen canopy were damaged. Damage also differed between canopy treatments in 2002 (n=58, p<0.0001). In that year, alfalfa under both a partial canopy and no canopy sustained lower rates of damage than those under a full canopy. The type of damage also differed between years. In 2001, damage was almost exclusively caused by insect feeding while damage during the 2002 season, was a mix of insect defoliation and desiccation.

Alfalfa survival in 2001 was generally very high (>90%) in all plots, and despite the differences in damage, alfalfa survival did not differ (p=0.09) between the canopy treatments (Figure 8-3). Plant survival was much lower for all treatments in 2002, likely resulting from the extreme T and low precipitation during the first month of the experiment in that year. With either partial or complete canopy removal, alfalfa survival was approximately double (p<0.01) that of plants under a full canopy. Most mortality in 2002 occurred in week 6 (following the period of very hot air T), with few additional plants dying between there and the experiment end, three weeks later.

Conclusions and Significance to Agroforestry

Alfalfa leaf T and D are both strongly coupled to air T. Humidity also had a significant effect on alfalfa D, but the separation in RH levels observed between the aspen canopy treatments was not likely large enough for it to be the dominant environmental factor in this plant-to-atmosphere gradient. In addition to air T differences, levels of direct PAR received by plants may act to modify leaf T and cause significant changes in alfalfa D. Plants shaded by an aspen overstory or under overcast skies were generally at the same T or cooler than the prevailing air T. Conversely, alfalfa leaves directly illuminated by the sun had a greater T than the air.

Alfalfa D decreased with increasing level of aspen canopy. This decrease in D would increase transpiration rates and photosynthetic gas exchange in sheltered plants and may contribute to an improvement in alfalfa growth. As a facilitative mechanism in agroforestry systems, however, reducing D must be balanced against the competitive effects of reduced PAR also resultant from the aspen overstory. The area of the boreal where this experiment was conducted experiences an average of only 1.4 days a year with air T above 30 °C (1970-2000 normal, Environment Canada), although the frequency of days above this T threshold has increased in the last decade. Therefore, leaf T and D may be of only minor significance to annual alfalfa production in most years. The limited evidence from the alfalfa growth data in this experiment suggests that over the entire growing season, alfalfa was either unaffected by the level of aspen cover (alfalfa mass in 2001, height and leaf number in both years), or was negatively affected by full or partial aspen canopy in comparison to plants grown in the open (alfalfa mass in 2002). Even with a significant threshold event affecting plant damage and mortality, such as from the very hot air T coupled with drought conditions in 2002, annual survival was still the lowest under a full aspen canopy. Thus, other factors such as reduced growth potential resulting from lower PAR, or greater risk from insect predation, override the benefits of the levels of aspen cover examined in preventing episodic T and D induced damage and mortality. This ultimately masks the incremental growth benefits of improved transpiration. Additionally, these results should be qualified by the canopy and light levels assessed, which do not represent the full range of range of treatments that could be considered in agroforestry systems. Nevertheless, these data do indicate that in environments with combinations of very high T and chronically low RH, partial tree cover may have greater annual significance to understory production. Likewise, plants with a lower light saturation level than alfalfa could experience less negative consequences from the aspen shading, and the facilitated lower leaf T and D, therefore, may take on greater importance to production and survival.

Table 8-1 Alfalfa (*Medicago sativa* L.) leaf temperature (T_L) and proportion of open sky photosynthetically active radiation (PAR) received at solar noon (± 0.5 hr) under boreal aspen with varying atmospheric conditions in 2001 and 2002. Values listed are the least squares means (adjusted standard error).

		Cloud Cover, Air Temperature			
	Aspen Canopy	**Clear, 36°C**	**Clear, 31 °C**	**Overcast, 20 °C**	**Overcast, 11 °C**
PAR* (%)	**Full**	12.8 (5.9) a	16.8 (5.9) a	No measure	17.5 (5.9) a
	Partial	28.2 (5.9) b	27.2 (5.9) b	No measure	35.0 (5.9) b
	None	78.0 (5.9) c	97.6 (5.9) c	No measure	91.9 (5.9) c
T_L# (°C)	**Full**	30.8 (1.3) a	27.7 (1.2) a	20.5 (0.3) a	10.2 (0.5) a
	Partial	35.4 (1.3) b	31.2 (1.2) ab	21.8 (0.3) b	11.2 (0.4) a
	None	41.2 (1.4) c	34.5 (1.2) b	22.0 (0.3) b	11.0 (0.4) a

* PAR means within a column followed by different letters are significantly different ($p<0.0001$).

# T_L means within a column followed by different letters are significantly different ($p<0.02$).

Table 8-2 Relationship of alfalfa (*Medicago sativa* L.) leaf temperature (T_L) and leaf-to-atmosphere vapour pressure difference (D) to air temperature (T_A), photosynthetically active radiation (PAR) and relative humidity (RH) under a boreal aspen canopy in 2001 and 2002.

Dependent Variable	**Adjusted Model R^2**	**Independent Variable**	**Partial R^2**	**Model R^2**	**B**[#]	**Prob > |T|***
T_L	0.97	T_A	0.94	0.94	1.42	<0.001
		PAR	0.03	0.97	0.01	<0.001
		RH	<0.01	0.97	0.28	0.08
D	0.85	T_A	0.68	0.68	0.45	<0.001
		PAR	0.15	0.83	0.002	<0.01
		RH	0.04	0.87	0.18	0.03
D	0.98	T_L	0.87	0.87	0.43	<0.001
		T_A	0.11	0.98	- 0.16	0.03
		RH	<0.01	0.98	0.06	0.06

[#] Regression coefficient.
* Probability of the T-test of whether inclusion of this variable improves the overall fit of the model.

Figure 8-1 Alfalfa (*Medicago sativa* L.) leaf-to-atmosphere vapour pressure differences under a boreal aspen canopy with varying atmospheric conditions in 2001 and 2002. Vertical lines on the bars indicate the standard error. Within the same sampling period, columns with the same letter are not significantly different from each other (p>0.05).

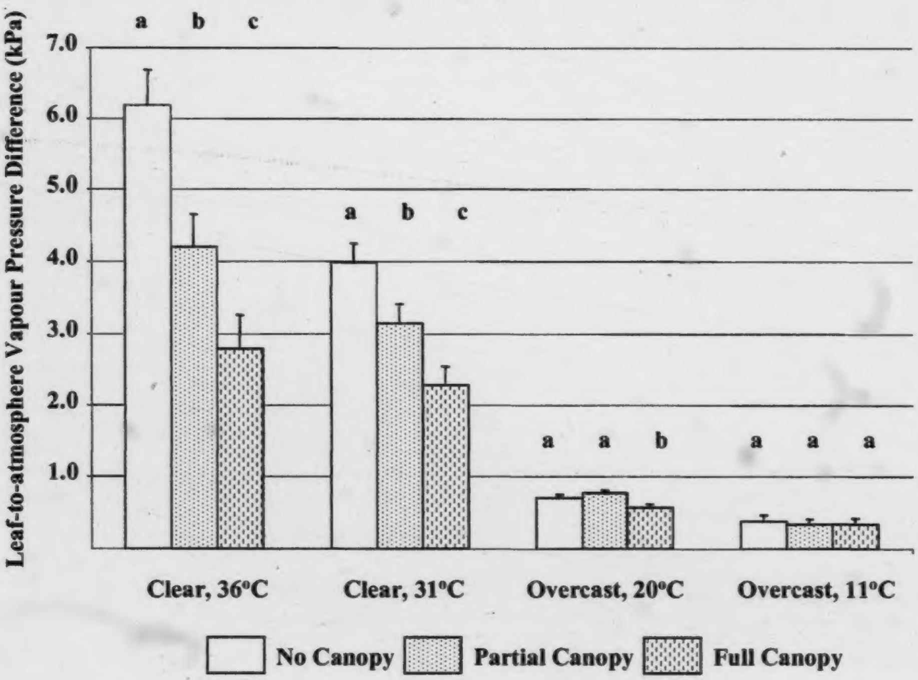


Figure 8-2 Difference between alfalfa (*Medicago sativa* L.) leaf temperature and boundary layer air temperature with varying atmospheric conditions in 2001 and 2002. Vertical lines on the bars indicate the standard error. Within the same sampling period, columns with the same letter are not significantly different from each other (p>0.05).

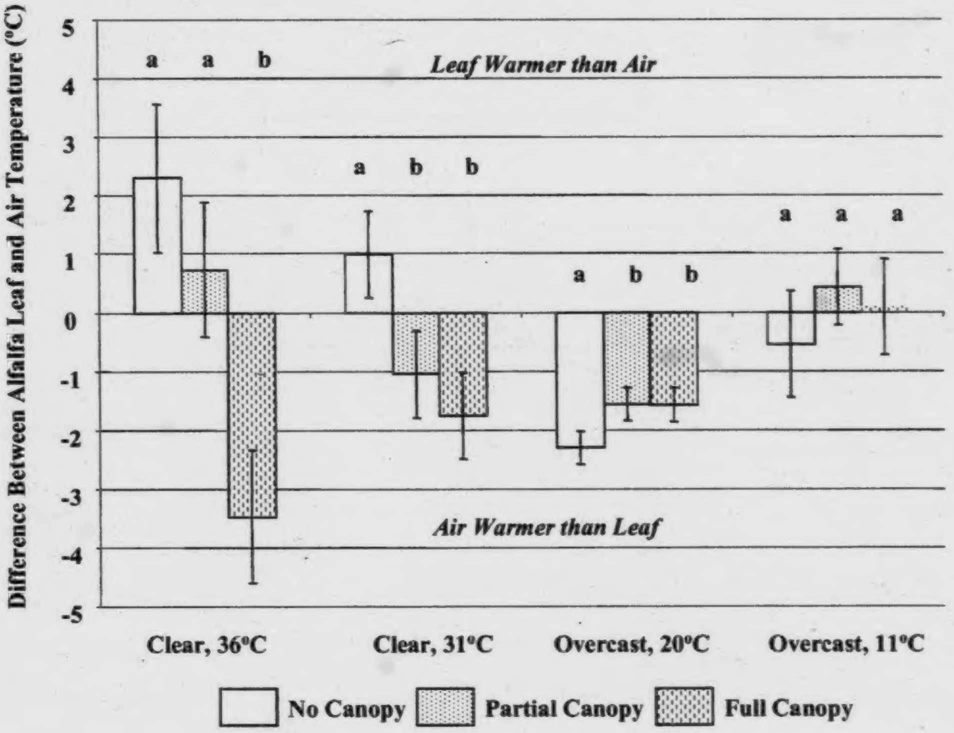
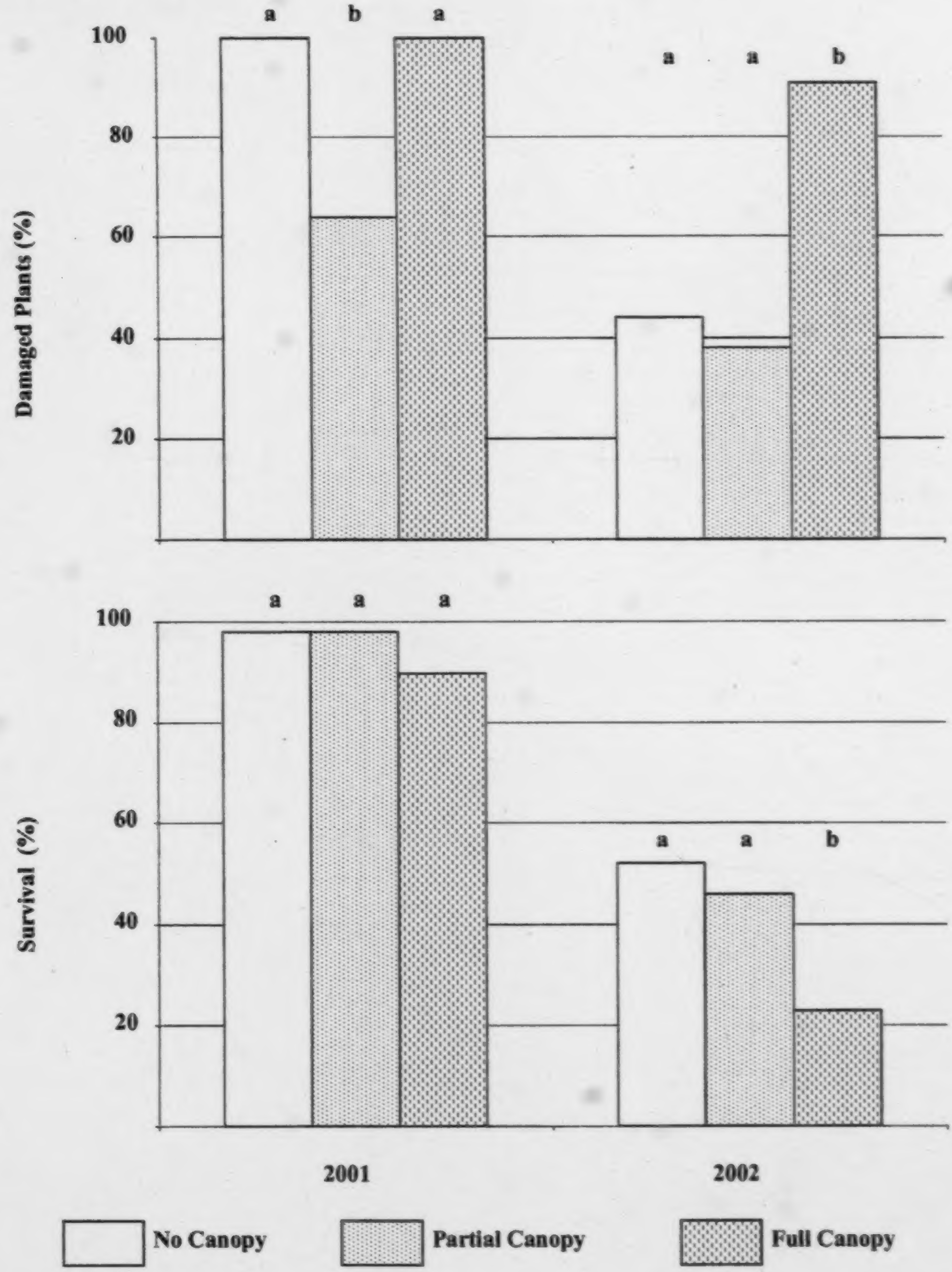


Figure 8-3 Alfalfa (*Medicago sativa* L.) damage and survival under boreal aspen, 2001-2002. Within the same year, columns with the same letter are not significantly different from each other ($p>0.05$).



8.5 Literature Cited

Al-Hamdani, S. and G.W. Todd. 1990. Effect of temperature regimes on photosynthesis, respiration, and growth in alfalfa. Proceeding of the Oklahoma Academy of Science 70: 1-4.

Clawson, K.L., R.D. Jackson and P.J. Pinter. 1989. Evaluating plant water stress with canopy temperature differences. Agronomy Journal 81: 858-863.

Dang, Q-L., H.A. Margolis, M.R. Coyea, M. Sy and G.J. Collatz. 1997. Regulation of branch level gas exchange of boreal trees: roles of shoot water potential and vapour pressure difference. Tree Physiology 17: 521-535.

Hogg, E.H., B. Saugier, J-Y. Pontailler, T.A. Black, W. Chen, P.A. Hurdle and A. Wu. 2000. Responses of trembling aspen and hazelnut to vapour pressure deficit in boreal deciduous forest. Tree Physiology 20: 725-734.

Jones, H.G. 1992. Plants and Microclimate, A Quantitative Approach to Environmental Plant Physiology. 2nd Edition, Cambridge University Press, Cambridge, U.K., 428 p.

Lin, C.H., R.L. McGraw, M.F. George and H.E. Garrett. 2001. Nutritive quality and morphological development under partial shade of some forage species with agroforestry potential. Agroforestry Systems 53: 269-281.

Littell, R.C., W.W. Stroup and R.J. Freund. 2002. SAS® for Linear Models, Fourth Edition. SAS Institute Inc., Cary, NC, 466 p.

McKenzie, J.S., R. Paquin and S.H. Duke. 1988. Cold and heat tolerance. Chapter 8 *in:* Hansen, A.A., D.K. Barnes and R.R. Hill, Jr. (editors). Alfalfa and Alfalfa Improvement. No. 29 in the series Agronomy, American Society of Agronomy Inc., Crop Science Society of America Inc. and Soil Science Society of America Inc., Madison, WI.

Reed, R. and R.L. Travis. 1987. Paraheliotropic leaf movement in mature alfalfa canopies. Crop Science 27: 301-304.

Strong, W.L. and K.R. Leggat. 1992. Ecoregions of Alberta. Alberta Forestry, Lands and Wildlife, Edmonton, AB, 59 p.

CHAPTER 9

Synthesis and General Conclusions

9.1 Results Synthesis - Relationship to Ecological Theory

This dissertation is based on the premise that ecological processes important to agroforestry production are a complex mix of competitive and facilitative effects. Moreover these effects can include both above- and below-ground processes, and can vary with a host of temporal, system and species-specific attributes. With so many factors potentially influencing production, this might lead to the conclusion that everything is important, or its corollary expressed in Commoner's first ecological law (Commoner 1972): "everything is interconnected." A complex linkage between all elements within these systems however, in no way negates the fact that some effects have demonstrated greater importance than others in determining production. Some of the results from these experiments conform to well-established principles of plant ecology and microclimatology. For example, predictable above-ground physical and microclimatic differences were observed in the understory in comparison to conditions in the open. Similarly expected, plant growth was closely linked to resource availability and microclimatic conditions. However, new perspectives on the importance of above- and below-ground processes and facilitation in northern ecosystems, and support for some general ecological theories also emerged.

Size Dependence

Size dependence was evident in plant-to-plant interactions, and was a function of the agroforest phase relative to the specific interaction in question. At the herbaceous phase, tree seedlings and herbaceous vegetation interacted symmetrically to plant size; net competitive interference of tree seedling growth correlated to larger above- and below-ground size of herbaceous species. Indeed, herbaceous biomass correlated to reductions in photosynthetically active radiation (PAR) reaching the trees and both herbaceous biomass and PAR availability correlated to aspen (*Populus tremuloides* Michx.) seedling growth. Below-ground competition for water or nutrients was also evident, and in absolute terms the greatest soil resource depletion was linked to marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.), the species with the greatest spatial dispersion of roots. However, there was not a tight correspondence between root mass concentrations and soil resource levels. This suggests other below-ground plant attributes (differences in root length per unit mass, rooting patterns, or absorption rates per unit root length) also have significant effects on the outcome of below-ground competition.

Above-ground processes in the arboreal phase were asymmetric, with the much larger trees controlling light availability and microclimate in the understory. No conclusions can be drawn from this research in regards to the symmetry of below-ground effects at the arboreal phase because neither root biomass nor patterns were measured in the aspen canopy removal – root trenching experiment.

The Balance Between Competition and Facilitation

True to the predictions of Callaway and Walker (1997), a mix of competitive and facilitative effects were observed in all experiments. The balance between these effects was highly dynamic, varying with species, site conditions and weather patterns. When viewed collectively, patterns in the relative strength and frequency of individual effects emerge (Table 9-1). Potentially competitive effects were generally large and consistent (e.g. reductions in PAR). In contrast, facilitation or potentially facilitative conditions occurred as either small, continuous effects (e.g. elevated humidity), or intermittent large effects (e.g. preventing a damage event or a radiative frost). Moreover, competition was observed in the absence of facilitation, but the potentially facilitative effects observed always occurred simultaneously with potentially competitive conditions. Thus, these results support the general theories on the importance of facilitation in relation to competition (Bertness and Callaway 1994, Brooker and Callaghan 1998, Holmgren *et al.* 1997): conditions for net facilitation were observed during what could be considered extremes in both environmental conditions (e.g. drought, temperature (T) extremes), and disturbance (e.g. animal damage to tree seedlings). In contrast, net competition occurred under prevailing 'normal' conditions.

On a site basis, the expression of net competition and facilitation on seasonal productivity also appeared to relate most to the system with the greatest occurrence of 'harsh' growing season conditions. Net competition was expressed in the herbaceous phase on aspen seedling growth, and in the arboreal phase in the Boreal, as evidenced by maximal growth when both above- and below-ground effects of competitors were removed. In contrast, a balance between potentially competitive and facilitative effects was observed in the Parkland which experienced the driest conditions, and the most frequent and severe high air T. Parkland above-ground net primary production (ANPP) in 2002 was comparable with a partial canopy to that of complete canopy removal. Since PAR reductions under the partial Parkland canopy were still negative for ANPP, in particular that of the grass species, it is probable that the Parkland understory was not light saturated with the partial canopy. Hence, it logically follows that facilitative effects compensated for the production differences due solely to lower PAR in order to create ANPP comparable to that of complete canopy removal.

A second general pattern also emerged: facilitation was more important for mitigating or preventing intermittent events than as continuous processes affecting growth. The importance of facilitation to the systems tested as an ecological process therefore, is secondary to the frequency and negative consequences of the unbuffered environmental conditions.

Dominance and Interaction of Above- and Below-ground Effects

Previous root-shoot separation studies have concluded below-ground competition is the predominant interaction influencing understory productivity, with evidence for neutral or net facilitation resulting from a partial tree cover. However, this evidence is predominantly from warm, dry, low latitude ecosystems. As observed by Rowe (1956) and again in these experiments, solar input appears to be the principle factor controlling aspen understory production differences in the Boreal. Solar input was also very important to Parkland understory dynamics, but it was relatively less of a factor in this warmer, drier ecosystem. In the Parkland, above-ground effects are still important to production, but they become potentially more facilitative (soil moisture conservation, climate moderation).

While the greatest changes in understory ANPP were in response to canopy removal, significant changes also resulted from reductions of root effects. Indeed, soil resources were an important factor for understory ANPP and cover, particularly among forbs. However, when below-ground effects were significant, they generally occurred with concomitant increases in PAR resulting from reductions in the aspen canopy. This response was exceptionally strong among the grass and sedge species and may indicate an interaction of above- and below-ground effects. Previous evidence for this type of interaction was noted in a review of root trenching studies in forested ecosystems (Coombs and Grubb 2000). In that review it was observed that when there was no understory response to removing root competition it was generally also associated with concomitant very low light levels. Cahill (1999) predicted these interactions would not occur when the understory species is adapted to low light conditions. However, in both the Parkland and Lower Boreal, the dominant grass species are adapted to open-growing conditions. Canopy removal could therefore increase photosynthetic activity and transpiration in understory species and with increased transpiration, soil water and nutrient availability could become limiting.

The interaction of above- and below-ground treatments supports a group of related ecological and agroforestry theories concerning limiting resources: Liebscher's 'law of the optimal' and it's derivatives, the theory of resource supply and demand (Davis *et al.* 1998), and Kho's (2000) second rule on resource availability in agroforestry systems (see Chapter 2, this volume). Moreover, the same potential for above- and below-ground interaction exists to influence the relative importance of facilitative effects, where the mode of facilitation is continuous and proportionate to photosynthesis. As observed under controlled conditions, reducing leaf-to-atmosphere vapour pressure difference (D) had a greater effect on some aspects of alfalfa (*Medicago sativa* L.) growth when applied in conjunction with higher PAR. This may mean that facilitative processes can be amplified with increased light availability up to a threshold level where insufficient tree cover remains to produce the facilitative microclimatic conditions. Likewise, facilitated increases in soil moisture should have proportionately larger effects on understory production with the higher growth activity associated at a higher PAR level. However, once again, an upper threshold setting an optimal balance for permitting greater light penetration versus the reduction in leaf litter production and blocking evaporation likely exists.

9.2 Management Implications

Implications for Agroforestry Design

Agroforestry design is an exercise in optimization on many different levels: biological, economic and social. Optimization in mixtures involve trade-offs from the maximum for any given component. Independent of positive non-production related externalities, a primary goal in agroforestry is to combine trees and understory crops such that total system production equals (balanced or neutral effects) or exceeds (overyields) that of equivalent areas in monocultures. Evidence from the early dynamics of aspen-forage plantations suggest neutral or net negative effects of combining aspen seedlings with herbaceous species. Agroforestry combinations during the establishment of aspen (i.e. herbaceous phase) will be limited by the strength of competition from herbaceous species. Species selection for compatibility is important and reduction of herbaceous competition through grazing, harvesting or other means must be considered for successful aspen agroforest establishment.

Both the Boreal and Parkland demonstrated potential for overyielding based on their microclimate profiles. With the exception of PAR, there were few growing season microclimatic differences between partial and full aspen canopies. Reducing aspen density doubled the amount of PAR reaching the understory (with associated increases in photosynthetic potential), but still retained many of the potentially facilitative microclimatic characteristics of a closed forest. Balancing facilitative and competitive effects for the design of agroforestry systems is therefore possible through further elucidation of the optimal level of aspen cover. With a partial canopy, understory production gains proportional to increased PAR availability do not come with the full negative consequences of an open microclimate.

In looking at both aspen and understory production however, there were contrasting production potentials between sites, and thus, different design considerations are necessary. The Boreal displayed the best aspen growth potential, but the least facilitation of understory growth. Lower tree densities, at the cost of reducing the tree crop, will be necessary in the Boreal to achieve the same level of understory production achieved with a partial aspen canopy. Alternately, planting higher yielding, shade tolerant forages in the Boreal understory may also improve overall system production. In contrast, the Parkland displayed the best understory forage crop potential, but also the least aspen growth. There are severe limitations to aspen production in the drier parts of the Parkland because of recurrent drought (Hogg and Hurdle 1995), as is expected in an ecosystem that naturally varies between aspen groves and open grassland. This effectively restricts viable aspen agroforestry operations to the mesic and hygric portions of the Parkland landscape. As a consequence, Parkland agroforestry may be best served by planting drought tolerant hybrid trees, rather than using extant aspen stands. Several tree species originally cultivated for wind breaks are now being examined for their agroforestry potential, and varieties are being developed that combine drought tolerance with rapid growth and suitable wood fibre quality. Fast growing hybrids would have the added advantage of reducing rotation length of the tree crop, which also might improve the economic returns from the wood crop. Moreover, rapid early growth minimizes the length of the herbaceous phase when trees are subject to competitive interference.

Implications for Pasture and Range Management

Independent of agroforestry opportunities, retaining tree cover in the Parkland can buffer the effects of a drought year on forage production. During the drought of 2002, the most severe recorded for the Parkland zone of Alberta, often the only forage sources remaining were in the understory of aspen stands. Experience from the drought provides a strong rationale for retaining tree cover to diversify the productive landbase in the Parkland. Year-to-year range production should be more consistent with the inclusion of forested rangelands where cyclical droughts are expected.

Pasture development in the Lower Boreal and Aspen Parkland often involves clearing large tracts of *Populus* dominated forests. This necessitates additional inputs and management during the first few years following clearing to counter the natural, vigorous vegetative reproduction of *Populus*. Moreover, unless cultivated or burned to rejuvenate these pastures on a regular basis, they often revert to dense forest cover as has already occurred on over 100,000 ha across the Canadian prairies (Kirychuk 2003). Partial aspen canopies at both sites greatly reduced aspen suckering in comparison to complete canopy removal. A silvopastoral approach may thereby improve pasture profits if forage production losses (if any) are offset by lower establishment and long-term maintenance costs.

Implications for Boreal Silviculture

In mixtures of tree seedlings and herbaceous vegetation, net competition was generally experienced by the tree seedlings by most measures of tree growth and performance, but not aspen survival. If maximum aspen production, or rapid early growth (to meet legal silvicultural obligations) is the sole management consideration, the benefits of vegetation control around tree seedlings is confirmed.

Chemical or mechanical weed control around aspen seedlings however, may require several plantation entries. This level of silvicultural activity can become prohibitively costly. Moreover, it exposes tree seedlings to the risk of physical or herbicide damage during stand tending work, elevates the risk of wind and water erosion on the exposed soils, reduces floral diversity, and may increase wind-throw if cultivation severs the shallow tree roots. Despite the potential for reduced initial tree growth therefore, there are still opportunities for using forages for vegetation control in aspen silviculture. This is particularly true if the alternative ground cover creates more intense competitive interference, such as from marsh reedgrass. Competitive interference was correlated to the biomass and PAR interception of the surrounding plants. Selection of a lower profile, lower yielding legume could provide the desired ground cover and nitrogen (N) fixation, without reducing light penetration, and thus should have less impact on aspen growth.

Aspen shelterwood systems have been recognized as a method to create a favourable microclimate for establishing spruce (*Picea glauca* (Moench) Voss) seedlings in comparison to boreal clearings (Man and Lieffers 1997). Results from these agroforestry experiments provide support for the physiological basis of employing shelterwood systems. Moreover, partial aspen overstory retention was sufficient to suppress the growth of marsh reedgrass, a problem species in Boreal silviculture. Shelterwood systems, in addition to climate modification, may produce less competition in the understory for spruce establishment than complete canopy removal, with sufficient aspen retention to dampen the growth of Boreal grasses.

9.3 Suggestions for Further Research

This research has set the foundation for further development of sustainable agroforestry systems for Canada, however, the complexity and variety of potential agroforestry configurations dictates that additional information is still required. A host of trials are needed to test agroforestry species combinations, variety and location effects, as well as the effects of tree density and spatial arrangement. In addition, new research emanating from the results of these experiments is needed in several key areas including:

1. the potential for plant mixtures to facilitate lower tree damage in new plantations;
2. long-term effects of management actions during agroforest establishment;
3. identifying thresholds (competitive and facilitative) in environmental conditions important for understory forage production;
4. the influence and interaction of livestock and other management practices on plant-to-plant processes; and,
5. socio-economic factors associated with various agroforestry options.

Aspen Damage

Research is needed to unambiguously confirm the relationship between plant mixtures and aspen seedling damage. In order to successfully separate tree size from sheltering effects, the experiment should be designed to employ trees of identical size placed within various levels of herbaceous plant cover (e.g. full, partial and no cover). If repeated on an annual basis, new trees of equivalent size (to compensate for growth differences emerging from variable competition) should be utilized each year. Frequent measures of tree growth relative damage can also confirm the size of trees when damaged, and the subsequent growth of damaged and undamaged trees.

Nutrient Retention Hypothesis

A potential trade-off between short- and long-term tree growth emerged from the N dynamics in mixtures of alfalfa and aspen seedlings. This theoretical trade-off raises the question of whether herbaceous vegetation can serve as a reservoir of nutrients in agroforests and how this relates to tree growth over longer periods (10 to 15 years). Soil nitrate (NO_3-N) was greatest in the absence of herbaceous competitors, however as evidenced by similar levels of available NO_3-N around solitary aspen with or without root barriers, aspen did not draw significantly on NO_3-N outside its immediate rooting zone. Without the presence of vegetation between trees this could lead to N-leakage from the system with a net loss that may have to be replaced to sustain desired tree growth rates. Herbaceous species draw on soil N (both within and outside of the zone used by the tree seedlings) and incorporate it into their biomass. This lowers available soil N, but potentially increases overall system N by preventing N losses. Nitrogen bound by herbaceous vegetation can be released back into the system when the tree canopy closes and suppresses understory growth leading to net mineralization. Thus, there may be some merit in balancing the short-term competitive effects from the presence of herbaceous species against longer-term facilitative effects on soil fertility.

Nutrient retention and turnover from the presence of ground cover in forests has limited support in previous research. McLaughlin *et al.* (1987) demonstrated that a legume cover crop was important for retaining and cycling N inputs throughout the whole rotation of hybrid poplar. Similarly, Prescott *et al.* (1996) found western red cedar (*Thuja plicata* Donn.) – western hemlock (*Tsuga heterophylla* (Raf.) Sarge) understory vegetation retained a greater portion of labelled N-fertilizer than those plots where understory vegetation was removed prior to fertilization. The greater system retention of the fertilizer however, came at the cost of a lower fraction of N in the target tree species. The potential benefits of nutrient retention relative to early competitive interference for long-term aspen growth require long-term evaluation of stands with and without cover crops.

The nutrient retention hypothesis can also be extended to include the relationship between understory productivity and forest cover. Removing aspen cover reduces leaf litter input and potentially alters nutrient cycling. Aspen stem and leaf litter plays a key role in regulating nutrient availability in boreal and north temperate ecosystems (Daubenmire 1953, Lieffers *et al.* 1996). The portion of nutrients captured by aspen is lost when these forests are cleared and may not be fully replaced by herbaceous species. As a consequence, the loss of annual aspen leaf litter input may lower system productivity, particularly on Luvisolic soils that have inherently low organic matter content. The long-term productivity of Boreal pastures without chemical fertilizer inputs is not well established and requires further investigation.

Evidence for the potential to facilitate tree growth from N fixed by legumes was inconclusive because of drought interference to alfalfa nodulation in 2002. As a result, research is still needed in the area of N-fixation and transfer from herbaceous crops to trees in northern agroforestry systems.

Understory Microclimate

Measures of alfalfa in the aspen understory revealed a linkage between leaf T, air T, and direct solar input (as measured by fractional PAR availability above the plants). Alfalfa leaves shaded by aspen or under overcast skies were generally at the same T or cooler than the prevailing air T. Conversely, alfalfa leaves directly illuminated by the sun had a greater T than the air. The importance of the net radiation balance to leaf T requires additional research. Moreover, all of these measures were made under conditions of very low or no wind. More robust modeling of leaf T and D under field conditions requires measures over a broader range and combination of air T, direct solar input and wind speeds.

Field measures also found a tenuous link between high alfalfa leaf T and D and alfalfa mortality in the ensuing weeks, but the mortality due to lethal leaf T could not be separated from drought effects in that period. Research under controlled conditions is therefore needed to establish the threshold leaf T of various potential understory crops beyond which irreparable damage occurs, and the frequency with which these conditions occur in different environments. Moreover, the relationship between D, leaf T and soil moisture regimes needs to be more clearly established.

Plant - Animal Interactions

Important aspects in many agroforestry systems not addressed by this research are the effects of livestock. Disturbance from herbivory, hoof action and other physical effects (e.g. rubbing) can potentially interact with all aspects of tree-forage dynamics. This additional level of complexity can either create additional challenges for successful integration of agriculture and forestry or, if properly managed, livestock can be used as a tool to mitigate negative effects and extend or accentuate facilitative effects. Potential livestock effects in aspen agroforestry systems in five broad areas require new information.

1. Impacts on competition in the herbaceous phase

Because livestock selectively graze preferred plant species, they can alter plant species composition and abundance. Plant competition in the herbaceous phase is symmetric and thus can be altered by removing plant cover with grazing. This can mitigate or eliminate competitive interference but must be balanced against the potential for tree damage. Moreover the timing of grazing can be used to accentuate facilitative aspects of herbaceous cover without letting the full competitive effects be expressed. For example, forages can be left intact during a drought to maintain a high ground cover for soil moisture conservation, and then grazed during periods of normal precipitation to reduce light interception.

2. Impacts on competition in the arboreal phase

Asymmetric overstory effects may be influenced by livestock and require investigation. Grazing reduces plant leaf area and carbohydrate reserves (used in regrowth after defoliation). This can potentially lower a plant's ability to capture resources and as a consequence, higher resource thresholds (light or soil resource availability) may be needed by grazed plants than ungrazed plants. This may necessitate a lower tree cover to generate sufficient growth potential to perpetuate a sustained understory yield where grazing weakens a plant's ability to gather soil resources.

3. Changes to species composition in the arboreal phase

Because animal selectively can influence understory plant composition, the potential to maintain understory plant species diversity requires investigation. For example, cattle are primarily grazers (preferring grass species). This selectivity for graminoids has the potential to reverse the observed trend of decreasing plant diversity from the increasing dominance of the key grass species in the Parkland.

4. Livestock damage to trees

Livestock can directly damage trees through browsing, rubbing and trampling. Aspen seedlings and saplings can be highly palatable to some livestock types and can be preferentially browsed. The incidence of browsing in agroforestry settings (where other preferred herbaceous species are present), and the efficacy of physical and chemical deterrents to reduce damage, relative to early plantation exclusion require further investigation. Trampling damage is generally a function of stocking density and tree size. Once trees attain sufficient size to become a physical and visual impediment to animal movement trampling damage is eliminated. The tree size - trampling damage relationship for aspen and related poplars with various livestock species is not well established.

5. Effects on soils

New information is needed on the degree to which Boreal and Parkland soils are compacted by livestock activity and the impact of this compaction on both tree and understory production. Aspen are shallow-rooted and sensitive to compaction resulting from mechanical harvesting, and therefore may also show a high degree of sensitivity to soil compaction by livestock. The degree and reversibility of compaction and its effects in agroforestry settings needs further research.

Many of the same aforementioned modifications to plant interactions could also be achieved by selective mechanical harvesting. Moreover, similar to the concerns for livestock management, new information is required on the methods, timing, frequency and intensity of mechanical harvesting, as well as the unintentional damage to tree and understory crops.

Socio-Economic Factors

Successful agroforestry depends on both the favourable combining of trees and herbaceous crops, and also on a host of social and economic factors that drive management decisions. Indeed, many rationales for adopting agroforestry systems are based purely in socio-economics. Some economic considerations requiring investigation with specific reference to Canadian crops and production potentials include:

1. relative value totals (Vandermeer 1989) of mixing different ratios of aspen and other crops in comparison to conventional agriculture or woodlot management;
2. the multi-year value of reducing infrequent production risks (e.g. drought) through agroforestry crop and landscape diversification;
3. cash flow and discount rates of agroforestry systems in comparison to conventional aspen woodlot management;
4. replacement values of inputs that agroforestry combinations replace (Vandermeer 1989), e.g. value of N-fixation replacing commercial fertilizer.
5. niche market opportunities for 'branded' agroforestry products given the preference among some consumers for products with tangible links to environmentally sensitive production.
6. the direct or indirect value of non-production related externalities (e.g. aesthetics, wildlife habitat, and diversity).

Likewise many barriers to adoption of agroforestry are rooted in long-standing personal and professional biases. Many Canadians believe we have inexhaustible natural resources (i.e. there is enough land for everyone to have exclusive domain of some area), or that there is irreconcilable incompatibility between conservation, agriculture and forest management. These beliefs are not shared in most of the world. A better understanding of what motivates producers and consumers, as well as the political, institutional and corporate barriers that act as disincentives for integrating and diversifying production are needed to fully assess the potential adoption of agroforestry systems.

Table 9-1 Summary of potentially competitive and facilitative effects in relation to agroforest phase, site and temporal variation.

	Phase/Ecosystem		
	Herbaceous	Arboreal	
Effect		**Parkland**	**Boreal**
Reduce PAR	C - -	C - -	C - -
Reduce Evaporation			
Normal precipitation	0	C +	0
Drought period	I + +	I + +	0
Water Uptake	C - -	C - -	C - -
Nutrient Deposition	C +	C +	0
Nutrient Uptake	C -	C -	C -
Shelter from Damage	I + +	nm	0
Increase Min T			
Average effect	nm	0	0
Effect on radiative frost	nm	I + +	I + +
Reduce Max T			
Average effect	nm	0	0
Effect on damaging heat	nm	I + +	I + +
Increase Humidity	nm	C +	C +

Occurrence: 'C'=continuous, 'I'=intermittent

Effect/size: 'nm' = not measured, '+' =small facilitative, '++' =large facilitative, '-' = small competitive, '--' = large competitive, '0'=neutral.

9.4 Literature Cited

Bertness, M.D. and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9: 191-193.

Brooker, R.W. and T.V. Callaghan. 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. Oikos 81: 196-207.

Cahill, J.F. Jr. 1999. Fertilization effects on interactions between above- and belowground competition in an old field. Ecology 80: 466-480.

Callaway, R.M. and L.R. Walker. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78: 1958-1965.

Commoner, B. 1972. The Closing Circle: Nature, Man and Technology. Knopf, New York, 326 p.

Coomes, D.A. and P.J. Grubb. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs 70(2): 171-207.

Daubenmire, R. 1953. Nutrient content of leaf litter of trees in the northern Rocky Mountains. Ecology 34: 786-793.

Davis, M.A., K.J. Wrage and P.B. Reich. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. Journal of Ecology 86: 652-661.

Holmgren, M., M. Scheffer and M.A. Huston. 1997. The interplay of facilitation and competition in plant communities. Ecology 78: 1966-1975.

Hogg, E.H. and P.A. Hurdle. 1995. The Aspen Parkland in western Canada: a dry-climate analogue for the future boreal forest? Water, Air and Soil Pollution 82: 381-400.

Kho, R.M. 2000. A general tree-environment-crop interaction equation for predictive understanding of agroforestry systems. Agriculture, Ecosystems and Environment 80: 87-100.

Kirychuk, B. 2003. Brush expansion on the Canadian prairies. Pages 10-11 *in*: Final Report of the Workshop on Integrated Brush Management, February 18-19, 2003, Saskatoon, Saskatchewan. Expert Committee on Forage Crops, Agriculture and Agri-food Canada.

Lieffers, V.J., K.J. Stadt, and S. Navratil. 1996. Age structure and growth of understory white spruce under aspen. Canadian Journal of Forest Research 26: 1002-1007.

Man, R. and V.J. Lieffers. 1997. Seasonal photosynthetic responses to light and temperature in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*) canopy and in the open. Tree Physiology 17: 437-444.

McLaughlin, R.A., E.A. Hansen and P.E. Pope. 1987. Biomass and nitrogen dynamics in an irrigated hybrid poplar plantation. Forest Ecology and Management 18: 169-188.

Perala, D.A. and D.H. Alban. 1982. Biomass, nutrient distribution and litterfall in *Populus*, *Pinus* and *Picea* stands on two different soils in Minnesota. Plant and Soil 64: 177-192.

Prescott, C.E., G.F. Weetman and J.E. Barker. 1996. Causes and amelioration of nutrient deficiencies in cutovers of cedar-hemlock forests in coastal British Columbia. The Forestry Chronicle 72: 293-302.

Rowe, J.S. 1956. Uses of undergrowth plant species in forestry. Ecology 37: 461-473.

Ruark, G.A. 1990. Evidence for the reserve shelterwood system for managing quaking aspen. Northern Journal of Applied Forestry 7: 58-62.

Vandermeer, J. 1989. The Ecology of Intercropping. Cambridge University Press, New York, 223 p.

APPENDIX 1

Indices for Measures of Competition

(1) **Competition Intensity** (Welden and Slauson 1986)

$$I = O - C$$

O = growth or survival under optimal conditions.
C = growth or survival in the presence of a competitor.

(2) **Importance of Competition** (Welden and Slauson 1986)

$$\mathrm{Im} = \left\{ \frac{O - C}{O - A} \right\}$$

O = growth or survival under optimal conditions.
C = growth or survival in the presence of a competitor.
A = growth or survival under other processes or conditions

(3) **Total Competitive Response** (Cahill 2002)

$$TCR = \ln\left(\frac{AN}{NN} \right)$$

AN = mean growth rate when grown with full above- or below-ground interaction with neighbour plants.
NN = mean growth rate when grown with no above- or below-ground interaction with neighbour plants.

(4) **Above-ground Competitive Response** (Cahill 2002)

$$ACR = \ln\left(\frac{SN}{NN} \right)$$

SN = mean growth rate when grown with full above-ground but not below-ground interaction with neighbour plants.
NN = mean growth rate when grown with no above- or below-ground interaction with neighbour plants.

(5) **Below-ground Competitive Response** (Cahill 2002)

$$BCR = \ln\left(\frac{RN}{NN}\right)$$

RN = mean growth rate when grown with full below-ground but not above-ground interaction with neighbour plants.

NN = mean growth rate when grown with no above- or below-ground interaction with neighbour plants.

Literature Cited

Cahill, J.F. Jr. 2002. Interactions between root and shoot competition vary among species. Oikos 99: 101-112.

Welden, C.W. and W.L. Slauson. 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Quarterly Review of Biology 61: 23-44.

APPENDIX 2

Analysis of Variance Tables

Table A2-1 Sources of variation and degrees of freedom for testing the effects of species replacement on focal aspen (*Populus tremuloides* Michx.) mass and leaf area in fixed-density mixtures with alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.).

Source of Variation	**Degrees of Freedom (df)**		**Adjusted Error df***
Perimeter Plant (P)	(p-1)	1	14.2
Error	p(r-1)	18	
Total	pr-1	19	

* Maximum error degrees of freedom from a Kenward-Roger correction (Kenward and Roger 1997).

Table A2-2 Sources of variation and degrees of freedom for testing the effects of species replacement on root mass concentration and soil nutrients under fixed-density mixtures of aspen (*Populus tremuloides* Michx.) seedlings, alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.).

Source of Variation	**Degrees of Freedom (df)**		**Error df***
Focal Plant (F)	(f-1)	2	149
Perimeter Plant (P)	(p-1)	2	149
Plot Position (O)	(o-1)	1	149
F x P	(f-1)(p-1)	4	149
F x O	(f-1)(o-1)	2	149
P x O	(p-1)(o-1)	2	149
F x P x O	(f-1)(p-1)(o-1)	4	149
Error	fpo(r-1)	162	
Total	fpor-1	179	

* Maximum error degrees of freedom from a Kenward-Roger correction.

Table A2-3 Sources of variation and degrees of freedom for analyzing the effects of mixtures of aspen (*Populus tremuloides* Michx.) seedlings, alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) on annual measures of aspen growth, indices of competition based on these measures, and photosynthetically active radiation.

Source of Variation	Degrees of Freedom (df)		Error df*
Focal Species (F)	(f-1)	2	79
Perimeter Species (P)	(p-1)	2	79
F x P	(f-1)(p-1)	4	79
Error a (within sampling periods)	fp(r-1)	81	
Year (Y)	(y-1)	1	79
Y x F	(y-1)(f-1)	2	79
Y x P	(y-1)(p-1)	2	79
Y x F x P	(y-1)(f-1)(p-1)	4	79
Error b (across sampling periods)	fp(r-1)(y-1)	81	
Total	yfpr-1	179	

* Maximum error degrees of freedom from a Kenward-Roger correction.

Table A2-4 Sources of variation and degrees of freedom for testing the effects of mixtures of aspen (*Populus tremuloides* Michx.) seedlings, alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) on repeated measures of soil moisture in 2002.

Source of Variation	Degrees of Freedom (df)		Error df*
Focal Species (F)	(f-1)	2	81
Perimeter Species (P)	(p-1)	2	81
F x P	(f-1)(p-1)	4	81
Error a (within sampling periods)	fp(r-1)	81	
Sampling Period (M)	(m-1)	3	243
M x F	(m-1)(f-1)	6	243
M x P	(m-1)(p-1)	6	243
M x F x P	(m-1)(f-1)(p-1)	12	243
Error b (across sampling periods)	fp(m-1)(r-1)	243	
Total	mfpr-1	359	

* Maximum error degrees of freedom from a Kenward-Roger correction.

Table A2-5 Sources of variation and degrees of freedom for testing above- and below-ground effects of alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) on aspen (*Populus tremuloides* Michx.) seedling mass and leaf area.

Source of Variation	**Degrees of Freedom (df)**		**Error df***
Species Composition (C)	(c-1)	2	93
Root Treatment (R)	(r-1)	1	93
Shoot Treatment (S)	(s-1)	1	93
C x R	(c-1)(r-1)	2	93
C x S	(c-1)(s-1)	2	93
S x R	(s-1)(r-1)	1	93
C x S x R	[(c-1)(s-1)(r-1)]-1**	1	93
Error	[crs(p-1)]-9**	99	
Total	[crsp-1]-10**	109	

* Maximum error degrees of freedom from a Kenward-Roger correction.
** df reduced for one species-root-shoot combination not tested.

Table A2-6 Sources of variation and degrees of freedom for testing above- and below-ground effects of alfalfa (*Medicago sativa* L.), marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) and aspen (*Populus tremuloides* Michx.) seedlings on root mass concentration and soil nutrients.

Source of Variation	**Degrees of Freedom (df)**		**Error df***
Species Composition (C)	(c-1)	2	179
Root Treatment (R)	(r-1)	1	179
Shoot Treatment (S)	(s-1)	1	179
Plot Position (O)	(o-1)	1	179
C x R	(c-1)(r-1)	2	179
C x S	(c-1)(s-1)	2	179
C x O	(c-1)(o-1)	2	179
S x R	(s-1)(r-1)	1	179
S x O	(s-1)(o-1)	1	179
R x O	(r-1)(o-1)	1	179
C x S x R	[(c-1)(s-1)(r-1)]-1**	1	179
C x S x O	(c-1)(r-1)(o-1)	2	179
C x R x O	(c-1)(s-1)(r-1)	2	179
O x S x R	(o-1)(r-1)(s-1)	1	179
C x S x R x O	[(c-1)(r-1)(s-1)(o-1)]-1**	1	179
Error	[crso(p-1)]-9**	207	
Total	[crsop-1]-11**	228	

* Maximum error degrees of freedom from a Kenward-Roger correction.
** df reduced for one species-root-shoot combination not tested.

Table A2-7 Sources of variation and degrees of freedom for testing the above- and below-ground effects of alfalfa (*Medicago sativa* L.) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) on repeated measures of aspen (*Populus tremuloides* Michx.) seedling growth.

Source of Variation	**Degrees of Freedom (df)**		**Error df***
Species Composition (C)	(c-1)	2	85.6
Root Treatment (R)	(r-1)	1	85.3
Shoot Treatment (S)	(s-1)	1	86.3
S x R	(s-1)(r-1)	1	86.6
C x R	(c-1)(r-1)	2	85.7
C x S	(c-1)(s-1)	2	85.6
C x S x R	[(c-1)(s-1)(r-1)]-1**	1	85.1
Error a (within years)	[crs(p-1)]-9**	99	
Year (Y)	(y-1)	1	93.5
Y x C	(c-1)(y-1)	2	93.4
Y x S	(s-1)(y-1)	1	93.5
Y x R	(r-1)(y-1)	1	93.4
Y x C x S	(c-1)(r-1)(y-1)	2	93.6
Y x S x R	(y-1)(r-1)(s-1)	1	93.4
Y x C x R	(y-1)(c-1)(r-1)	2	93.4
Y x C x S x R	[(c-1)(r-1)(s-1)(y-1)]-1**	1	93.8
Error b (between years)	[crs(y-1)(p-1)]-9**	99	
Total	[crsyp-1]-20**	219	

* Maximum error degrees of freedom from a Kenward-Roger correction.
** df reduced for one species-root-shoot combination not tested.

Table A2-8 Sources of variation and degrees of freedom for testing above- and below-ground effects of alfalfa (*Medicago sativa* L.), marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) and aspen (*Populus tremuloides* Michx.) seedlings on repeated measures of soil moisture.

Source of Variation	Degrees of Freedom (df)		Error df*
Species Composition (C)	(c-1)	2	154
Root Treatment (R)	(r-1)	1	147
Shoot Treatment (S)	(s-1)	1	149
Plot Position (O)	(o-1)	1	149
C x R	(c-1)(r-1)	2	147
C x S	(c-1)(s-1)	2	146
C x O	(c-1)(o-1)	2	154
S x R	(s-1)(r-1)	1	148
S x O	(s-1)(o-1)	1	150
R x O	(r-1)(o-1)	1	150
C x S x R	[(c-1)(s-1)(r-1)]-1**	1	146
C x S x O	(c-1)(s-1)(o-1)	2	146
C x R x O	(c-1)(r-1)(o-1)	2	150
S x R x O	(s-1)(r-1)(o-1)	1	150
C x R x S x O	[(c-1)(r-1)(s-1)(o-1)]-1**	1	147
Error a (within periods)	[crso(p-1)]-9**	207	
Sampling Period (M)	(m-1)	3	476
M x C	(m-1)(c-1)	6	467
M x S	(m-1)(s-1)	3	478
M x R	(m-1)(r-1)	3	469
M x O	(m-1)(o-1)	3	483
M x C x R	(m-1)(c-1)(r-1)	6	459
M x C x S	(m-1)(c-1)(s-1)	6	459
M x C x O	(m-1)(c-1)(o-1)	6	459
M x S x R	(m-1)(s-1)(r-1)	3	470
M x S x O	(m-1)(s-1)(o-1)	3	459
M x R x O	(m-1)(r-1)(o-1)	3	459
M x C x S x R	[(m-1)(c-1)(s-1)(r-1)]-3**	3	459
M x C x S x O	(m-1)(c-1)(s-1)(o-1)	6	459
M x C x R x O	(m-1)(c-1)(r-1)(o-1)	6	459
M x S x R x O	(m-1)(s-1)(r-1)(o-1)	3	459
M x C x S x R x O	[(m-1)(c-1)(s-1)(r-1)(o-1)]-3**	3	459
Error b (across periods)	[crso(m-1)(p-1)]-27**	621	
Total	[crsomp-1]-40**	919	

* Maximum error degrees of freedom from a Kenward-Roger correction.

** df reduced for one species-root-shoot combination not tested.

Table A2-9 Sources of variation and degrees of freedom for testing the daily effects of aspen (*Populus tremuloides* Michx.) canopies on subcanopy air temperature and humidity.

Source of Variation	Degrees of Freedom (df)		Error df*
Site (S)	(s-1)	1	12
Canopy Removal (C)	(c-1)	2	12
S x C	(s-1)(c-1)	2	12
Error	sc(r-1)	12	
Total	scr-1	17	

* Kenward-Roger correction applied to error degrees of freedom

Table A2-10 Sources of variation and degrees of freedom for testing the effects of aspen (*Populus tremuloides* Michx.) canopies on repeated annual measures subcanopy air temperature, relative humidity and photosynthetically active radiation at peak aspen leaf area.

Source of Variation	Degrees of Freedom (df)		Error df*
Site (S)	(s-1)	1	12
Canopy Removal (C)	(c-1)	2	12
S x C	(s-1)(c-1)	2	12
Error a (within years)	sc(r-1)	12	
Year (Y)	(y-1)	2	24
S x Y	(y-1)(s-1)	2	24
C x Y	(y-1)(c-1)	4	24
S x C x Y	(y-1)(s-1)(c-1)	4	24
Error a (between years)	sc(y-1)(r-1)	24	
Total	scyr-1	53	

* Maximum error degrees of freedom from a Kenward-Roger correction.

Table A2-11 Sources of variation, degrees of freedom and error terms for the analyses of variance testing the effects of aspen (*Populus tremuloides* Michx.) canopy removal and root trenching on repeated measures of soil moisture.

Source of Variation	**Degrees of Freedom (df)**		**Error df[*]**
Mainplot			
Site (S)	(s-1)	1	12
Canopy Removal (C)	(c-1)	2	12
S x C	(c-1)(s-1)	2	12
Main Plot Error	cs(r-1)[#]	12	
Subplots			
Trenching (T)	t-1	2	67.3
T x C	(t-1)(c-1)	4	67.3
T x S	(t-1)(s-1)	2	67.3
T x C x S	(t-1)(c-1)(s-1)	4	67.3
Subplot Error	[sct(rv-1)]-[sc(r-1)][**]	78	
Sampling Period (M)	(m-1)	8	610
M x S	(m-1)(s-1)	8	610
M x C	(m-1)(c-1)	16	610
M x T	(m-1)(t-1)	16	610
M x S x C	(m-1)(s-1)(c-1)	16	610
M x S x T	(m-1)(s-1)(t-1)	16	610
M x C x T	(m-1)(c-1)(t-1)	32	610
M x S x C x T	(m-1)(s-1)(c-1)(t-1)	32	610
Error c (Between Periods)	sct(rv-1)(m-1)	630	
Total	sctrvm-1	863	

[*] Maximum error degrees of freedom from a Kenward-Roger correction.
[#] r = replication of the canopy removal treatments = 3
[**] v = replication of the root trenching treatments = 2

Table A2-12 Sources of variation, degrees of freedom and error terms for the analyses of variance testing the effects of aspen (*Populus tremuloides* Michx.) canopy removal and root trenching on repeated measures of soil nitrogen.

Source of Variation	**Degrees of Freedom (df)**		**Error df***
Mainplot			
Site (S)	(s-1)	1	12
Canopy Removal (C)	(c-1)	2	12
S x C	(c-1)(s-1)	2	12
Main Plot Error	cs(r-1)#	12	
Subplots			
Trenching (T)	t-1	2	78
T x C	(t-1)(c-1)	4	78
T x S	(t-1)(s-1)	2	78
T x C x S	(t-1)(c-1)(s-1)	4	78
Subplot Error	[sct(rv-1)]-[sc(r-1)]**	78	
Sampling Period (M)	(m-1)	1	90
M x S	(m-1)(s-1)	1	90
M x C	(m-1)(c-1)	2	90
M x T	(m-1)(t-1)	2	90
M x S x C	(m-1)(s-1)(c-1)	2	90
M x S x T	(m-1)(s-1)(t-1)	2	90
M x C x T	(m-1)(c-1)(t-1)	4	90
M x S x C x T	(m-1)(s-1)(c-1)(t-1)	4	90
Error c (Between Periods)	sct(rv-1)(m-1)	90	
Total	sctrvm-1	215	

[*] Maximum error degrees of freedom from a Kenward-Roger correction.
[#] r = replication of the canopy removal treatments = 3
[**] v = replication of the root trenching treatments = 2

Table A2-13 Sources of variation and degrees of freedom for testing the effects of canopy removal on aspen (*Populus tremuloides* Michx.) growth from 2000 to 2002.

Source of Variation	Degrees of Freedom (df)		Error df*
Site (S)	(s-1)	1	8
Canopy Removal (C)	(c-1)	1	8
S x C	(s-1)(c-1)	1	8
Error	sc(r-1)	8	
Total	scr-1	11	

* Maximum error degrees of freedom from a Kenward-Roger correction.

Table A2-14 Sources of variation and degrees of freedom for testing the effects of canopy removal on repeated measures of aspen (*Populus tremuloides* Michx.) density, height, diameter, and basal area.

Source of Variation	Degrees of Freedom (df)		Error df*
Site (S)	(s-1)	1	12
Canopy Removal (C)	(c-1)	2	12
S x C	(s-1)(c-1)	2	12
Error a (within years)	sc(r-1)	12	
Year	(y-1)	2	24
Y x S	(y-1)(s-1)	2	24
Y x C	(y-1)(c-1)	4	24
Y x S x C	(y-1)(s-1)(c-1)	4	24
Error b (between years)	sc(y-1)(r-1)	24	
Total	scyr-1	53	

* Maximum error degrees of freedom from a Kenward-Roger correction.

Table A2-15 Sources of variation, degrees of freedom and error terms for the analyses of variance testing the effects of aspen (*Populus tremuloides* Michx.) canopy removal and root trenching on repeated annual measures of understory vascular plant cover, above-ground net primary production and diversity.

Source of Variation	Degrees of Freedom (df)		Error df*
Mainplot			
Site (S)	(s-1)	1	12
Canopy Removal (C)	(c-1)	2	12
S x C	(c-1)(s-1)	2	12
Main Plot Error	cs(r-1)#	12	
Subplots			
Trenching (T)	t-1	2	78
T x C	(t-1)(c-1)	4	78
T x S	(t-1)(s-1)	2	78
T x C x S	(t-1)(c-1)(s-1)	4	78
Subplot Error	[sct(rv-1)]-[sc(r-1)]**	78	
Year (Y)	(y-1)	2	180
Y x S	(y-1)(s-1)	2	180
Y x C	(y-1)(c-1)	4	180
Y x T	(y-1)(t-1)	4	180
Y x S x C	(y-1)(s-1)(c-1)	4	180
Y x S x T	(y-1)(s-1)(t-1)	4	180
Y x C x T	(y-1)(c-1)(t-1)	8	180
Y x S x C x T	(y-1)(s-1)(c-1)(t-1)	8	180
Error c (Between Periods)	sct(rv-1)(y-1)	180	
Total	sctrvy-1	323	

[*] Maximum error degrees of freedom from a Kenward-Roger correction.

[#] r = replication of the canopy removal treatments = 3

[**] v = replication of the root trenching treatments = 2

Table A2-16 Sources of variation, degrees of freedom and error terms for the multivariate analysis of variance testing the effects of aspen (*Populus tremuloides* Michx.) canopy removal and root trenching on the difference in relative yields of forbs, graminoids and shrubs from 2000 to 2002.

Source of Variation	**Degrees of Freedom**		**Error df**
Mainplot			
Site (S)	s-1	1	
Canopy Removal (C)	c-1	2	
B x C Interaction	(c-1)(s-1)	2	
Main Plot Error	cs(r-1)[#]	2	
Subplots			
Trenching (T)	t-1	2	
T x C Interaction	(t-1)(c-1)	4	
T x B Interaction	(t-1)(s-1)	2	
T x C x B Interaction	(t-1)(c-1)(s-1)	4	
Subplot Error	[sct(rv-1)]-[sc(r-1)][*]	78	
Total	bctrv-1	107	
MANOVA tests**			
S		3	76
C		6	152
S x C		6	152
T		6	152
S x T		6	152
C x T		12	201
S x C x T		12	201

[#] r = replication of the canopy removal treatments = 3

[*] v = replication of the root trenching treatments = 2

** Wilk's Lambda

Table A2-17 Sources of variation and degrees of freedom for testing the effects of relative humidity and photosynthetically active radiation on alfalfa (*Medicago sativa* L.) mass and leaf area.

Source of Variation	**Degrees of Freedom (df)**		**Error df***
Humidity (H)	(h-1)	1	6
Main Plot error	h(r-1)	6	
PAR (P)	(p-1)	1	10
H x P	(h-1)(p-1)	1	10
Error	hp(r-1)	12	
Total	hpr-1	15	

* Maximum error degrees of freedom from a Kenward-Roger correction.

Table A2-18 Sources of variation and degrees of freedom for testing the effects of relative humidity and photosynthetically active radiation on repeated measures of alfalfa (*Medicago sativa* L.) growth.

Source of Variation	**Degrees of Freedom (df)**		**Error df***
Humidity (H)	(h-1)	1	6
Main Plot error	h(r-1)	6	
PAR (P)	(p-1)	1	10.8
H x P	(h-1)(p-1)	1	10.8
Subplot Error	hp(r-1)	12	
Week (W)	(w-1)	4	35.6
W x H	(w-1)(h-1)	4	35.6
W x P	(w-1)(p-1)	4	35.6
W x H x P	(w-1)(h-1)(p-1)	4	35.6
Error c (between weeks)	hp(r-1)(w-1)	48	
Total	hprw-1	79	

* Maximum error degrees of freedom from a Kenward-Roger correction.

Table A2-19 Source, degrees of freedom and error terms for the analyses of variance testing the effects of aspen canopy removal on understory alfalfa (*Medicago sativa* L.) leaf temperature and leaf-to-atmosphere vapour pressure difference.

Source of Variation	**Degrees of Freedom (df)**		**Error df***
Canopy Removal	c-1	2	6
Experimental Error	c(r-1)	6	
Subsampling Error **	cr(s-1)	135	
Total **	crs-1	143	

* Maximum error degrees of freedom from a Kenward-Roger correction.
** Subject to variable sample size for each response variable due to missing values.

Literature Cited

Kenward, M.G., and Roger, J.H. 1997. Small sample inference for fixed effects from restricted maximum likelihood. Biometrics 53: 983-997.

APPENDIX 3

Canopy Cover of Vascular Plant Species: Aspen Canopy Removal and Root Trenching Experiment

Table A3-1 Trace[1] vascular plant species at Kinsella from 2000 to 2002.

Forbs
Anemone canadensis
Aster ciliolatus
Convolvulus arvense
Circium arvense
Chenopodium album
Fragaria virginiana
Geum allepicum
Lapula echinata
Lathyrus occidentalis
Medicago sativa
Mentha arvensis
Ranunculus acris
Sonchus arvensis
Stellaria longifolia

Graminoids
Carex spp.
Hordeum jubatum

Tall Shrubs (>1-m tall)
Prunus virginiana
Rosa acicularis

Low Shrubs (<1-m tall)
Cornus stolonifera
Prunus virginiana

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[1] <0.5% average canopy cover throughout the experiment.

Table A3-2 Effects of aspen (*Populus tremuloides* Michx.) canopy and root trenching on canopy cover (%) of prominent vascular plant species at Kinsella from 2000 to 2002. Values are the arithmetic means (standard error).

Level of Canopy	Root Trenching	*Amelanchier alnifolia* (>1 m tall) 2000		2001		2002		*Amelanchier alnifolia*(<1 m tall) 2000		2001		2002	
Full	TB[1]	3.3	(4.7)	2.5	(1.6)	5.8	(4.6)	2.1	(2.9)	0.4	(0.6)	2.1	(1.7)
	TNB[2]	5.8	(4.6)	4.2	(3.8)	10.8	(7.4)	2.1	(2.9)	0.8	(1.2)	5.4	(4.3)
	UT[3]	4.2	(5.9)	1.7	(2.4)	3.7	(3.4)	0.8	(1.2)	1.8	(1.8)	6.3	(5.1)
Part	TB	1.7	(1.5)	2.5	(3.5)	6.7	(9.4)	0.0	(0.0)	0.2	(0.2)	4.2	(5.9)
	TNB	9.5	(8.1)	5.3	(5.7)	6.7	(6.7)	0.0	(0.0)	0.0	(0.0)	2.4	(2.9)
	UT	8.7	(11.7)	5.0	(7.1)	5.0	(5.8)	2.9	(3.5)	4.6	(6.5)	7.1	(6.4)
None	TB	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)
	TNB	0.0	(0.0)	0.8	(1.2)	3.2	(3.4)	0.0	(0.0)	0.0	(0.0)	0.8	(1.2)
	UT	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)
		Ribes hirtellum (<1 m tall) 2000		2001		2002		*Rosa acicularis* (<1 m tall) 2000		2001		2002	
Full	TB	0.4	(0.6)	1.0	(0.9)	3.3	(3.0)	0.4	(0.6)	3.3	(4.0)	2.7	(2.2)
	TNB	0.8	(0.8)	0.8	(1.2)	0.4	(0.6)	0.4	(0.6)	0.3	(0.3)	0.3	(0.3)
	UT	2.9	(4.1)	8.3	(7.7)	4.2	(4.1)	0.8	(0.7)	4.9	(4.2)	2.8	(1.8)
Part	TB	3.3	(2.9)	0.7	(0.4)	0.8	(0.7)	0.8	(1.2)	3.4	(3.0)	2.3	(1.9)
	TNB	1.8	(2.6)	7.1	(6.5)	4.1	(5.2)	14.7	(7.9)	10.8	(5.1)	6.6	(3.9)
	UT	8.1	(5.7)	13.9	(10.4)	8.9	(8.1)	8.4	(5.9)	10.2	(5.8)	6.5	(4.0)
None	TB	0.0	(0.0)	0.1	(0.1)	0.6	(0.6)	3.3	(3.1)	0.6	(0.6)	0.8	(0.6)
	TNB	0.0	(0.0)	0.4	(0.3)	0.2	(0.2)	8.8	(6.8)	1.3	(1.8)	2.8	(3.1)
	UT	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.2	(0.1)	2.3	(1.9)	4.4	(3.7)

Table A3-2 continued.

Level of Canopy	Root Trenching	*Rubus idaeus* (<1 m tall) 2000	2001	2002	*Symphoricarpos occidentalis* (<1 m tall) 2000	2001	2002
Full	TB^1	1.3 (1.2)	1.1 (0.9)	1.2 (1.1)	12.7 (7.5)	12.9 (4.9)	15.3 (7.1)
	TNB^2	2.9 (4.1)	6.3 (7.7)	1.8 (2.0)	13.8 (7.5)	10.5 (2.3)	15.0 (4.7)
	UT^3	0.8 (0.7)	1.8 (1.4)	0.2 (0.2)	10.2 (4.8)	26.3 (14.5)	16.8 (6.4)
Part	TB	5.8 (5.9)	9.3 (8.4)	1.8 (1.2)	10.1 (5.3)	8.2 (2.4)	6.6 (1.8)
	TNB	3.3 (3.5)	6.7 (6.2)	5.4 (4.9)	9.3 (4.0)	9.8 (3.3)	8.1 (3.5)
	UT	8.8 (8.8)	11.3 (10.2)	4.2 (4.6)	17.5 (7.2)	12.3 (5.9)	10.8 (5.8)
None	TB	2.5 (3.5)	11.4 (12.7)	3.3 (3.0)	5.5 (1.9)	6.8 (4.5)	9.1 (3.8)
	TNB	4.2 (4.1)	5.1 (5.8)	1.6 (1.7)	10.0 (3.3)	8.1 (2.0)	15.6 (8.4)
	UT	10.0 (14.1)	11.7 (14.5)	5.0 (7.1)	10.6 (9.8)	9.5 (5.1)	14.1 (6.4)

		Actae rubra 2000	2001	2002	*Aster laevis* 2000	2001	2002
Full	TB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	5.1 (5.7)	0.4 (0.6)	0.9 (0.9)
	TNB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.6 (0.8)	0.0 (0.0)
	UT	0.8 (1.2)	0.0 (0.0)	0.2 (0.2)	2.7 (2.8)	2.9 (3.5)	0.0 (0.0)
Part	TB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.2	6.6 (4.5)	0.2 (0.2)
	TNB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.8 (1.8)	0.6 (0.8)
	UT	0.0 (0.0)	0.0 (0.0)	0.6 (0.8)	0.0 (0.0)	0.6 (0.6)	0.0 (0.0)
None	TB	6.7 (9.4)	4.2 (5.9)	0.4 (0.6)	0.2 (0.2)	14.0 (10.3)	0.8 (1.2)
	TNB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.2	4.3 (2.1)	0.0 (0.0)
	UT	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.4 (0.5)	0.0 (0.0)

Table A3-2 continued.

Level of Canopy	Root Trenching	*Galium boreale* 2000	*Galium boreale* 2001	*Galium boreale* 2002	*Lysimachia ciliata* 2000	*Lysimachia ciliata* 2001	*Lysimachia ciliata* 2002
Full	TB[1]	0.1 (0.1)	0.5 (0.5)	0.2 (0.2)	0.0 (0.0)	4.3 (5.8)	4.0 (3.7)
	TNB[2]	0.2 (0.2)	0.8 (0.8)	1.8 (1.7)	0.0 (0.0)	0.4 (0.6)	0.0 (0.0)
	UT[3]	0.6 (0.3)	1.2 (0.8)	1.3 (1.4)	0.0 (0.0)	0.2 (0.2)	0.3 (0.3)
Part	TB	1.0 (0.8)	0.7 (0.5)	0.7 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	TNB	0.5 (0.4)	0.5 (0.3)	0.8 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	UT	0.7 (0.7)	0.8 (0.6)	1.2 (1.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
None	TB	0.3 (0.2)	1.8 (1.3)	0.6 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	TNB	0.3 (0.2)	0.3 (0.2)	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	UT	0.3 (0.2)	3.3 (3.3)	1.0 (1.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		Scutellaria gallericulata			***Smilacina stellata***		
		2000	**2001**	**2002**	**2000**	**2001**	**2002**
Full	TB	0.0 (0.0)	0.2 (0.2)	2.4 (1.6)	3.3 (4.7)	0.8 (0.8)	0.0 (0.0)
	TNB	0.0 (0.0)	0.0 (0.0)	2.1 (2.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	UT	0.0 (0.0)	0.0 (0.0)	4.2 (5.9)	0.2 (0.2)	0.6 (0.6)	0.0 (0.0)
Part	TB	0.4 (0.6)	0.8 (1.2)	2.0 (1.7)	0.0 (0.0)	0.0 (0.0)	0.4 (0.6)
	TNB	3.5 (3.7)	2.5 (3.5)	0.8 (0.6)	0.0 (0.0)	0.0 (0.0)	0.6 (0.8)
	UT	0.0 (0.0)	1.8 (2.3)	0.0 (0.0)	1.4 (1.2)	0.0 (0.0)	0.4 (0.6)
None	TB	0.0 (0.0)	0.2 (0.2)	2.7 (2.9)	0.0 (0.0)	0.0 (0.0)	0.4 (0.6)
	TNB	0.0 (0.0)	1.3 (1.8)	3.2 (1.2)	0.0 (0.0)	0.0 (0.0)	0.4 (0.6)
	UT	0.0 (0.0)	0.0 (0.0)	1.8 (1.4)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)

Table A3-2 continued.

Level of Canopy	Root Trenching	*Stachys palustris* 2000	*Stachys palustris* 2001	*Stachys palustris* 2002	*Taraxacum officinale* 2000	*Taraxacum officinale* 2001	*Taraxacum officinale* 2002
Full	TB[1]	0.0 (0.0)	0.2 (0.2)	0.0 (0.0)	0.2 (0.2)	2.3 (1.3)	0.5 (0.5)
	TNB[2]	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.1 (2.9)	0.3 (0.2)	0.0 (0.0)
	UT[3]	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.4 (0.2)	0.6 (0.6)	0.0 (0.0)
Part	TB	0.0 (0.0)	1.0 (0.9)	0.0 (0.0)	1.1 (0.8)	2.1 (1.4)	0.0 (0.0)
	TNB	0.8 (1.2)	6.7 (8.7)	0.0 (0.0)	0.4 (0.6)	1.7 (1.3)	0.0 (0.0)
	UT	3.3 (4.7)	3.3 (4.7)	0.0 (0.0)	0.3 (0.4)	0.8 (0.7)	0.0 (0.0)
None	TB	0.0 (0.0)	0.4 (0.6)	0.0 (0.0)	0.5 (0.6)	0.0 (0.0)	0.1 (0.1)
	TNB	0.0 (0.0)	4.2 (5.9)	0.0 (0.0)	0.4 (0.6)	4.0 (3.0)	1.2 (1.4)
	UT	0.0 (0.0)	1.0 (1.4)	0.0 (0.0)	0.1 (0.1)	0.5 (0.6)	0.0 (0.0)

Level of Canopy	Root Trenching	*Thalictrum venulosum* 2000	*Thalictrum venulosum* 2001	*Thalictrum venulosum* 2002	*Vicia americana* 2000	*Vicia americana* 2001	*Vicia americana* 2002
Full	TB	0.3 (0.2)	1.3 (0.7)	0.5 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	TNB	1.3 (1.1)	4.7 (2.7)	2.4 (1.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	UT	1.8 (1.4)	2.9 (2.1)	1.3 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Part	TB	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.4 (0.6)	0.4 (0.6)	0.0 (0.0)
	TNB	4.7 (5.8)	2.3 (2.9)	0.8 (1.2)	2.1 (2.9)	3.8 (5.3)	0.0 (0.0)
	UT	2.2 (2.0)	2.8 (2.9)	1.4 (1.7)	0.0 (0.0)	0.6 (0.8)	0.0 (0.0)
None	TB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.7 (2.4)	1.7 (2.4)	0.0 (0.0)
	TNB	1.4 (1.7)	2.3 (1.9)	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	UT	0.8 (0.8)	0.7 (0.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

Table A3-2 continued.

Level of Canopy	Root Trenching	*Agropyron* spp.[4] 2000	*Agropyron* spp.[4] 2001	*Agropyron* spp.[4] 2002	*Bromus inermis* 2000	*Bromus inermis* 2001	*Bromus inermis* 2002
Full	TB[1]	5.2 (6.3)	4.2 (1.9)	1.4 (1.2)	0.5 (0.4)	2.9 (3.4)	9.6 (7.0)
	TNB[2]	1.9 (2.6)	1.3 (1.0)	1.3 (1.2)	6.0 (4.5)	2.1 (1.3)	16.7 (7.6)
	UT[3]	3.2 (3.4)	3.9 (4.0)	1.8 (1.1)	2.5 (3.1)	1.4 (0.8)	4.9 (3.0)
Part	TB	4.6 (3.1)	3.4 (2.5)	3.0 (2.8)	0.4 (0.4)	8.2 (7.8)	9.9 (5.3)
	TNB	5.3 (2.5)	2.7 (2.4)	1.8 (1.2)	0.4 (0.6)	9.7 (7.1)	14.8 (3.3)
	UT	4.2 (2.3)	2.3 (2.3)	1.0 (0.9)	0.5 (0.5)	7.8 (4.3)	7.8 (2.8)
None	TB	2.0 (2.3)	0.9 (1.3)	0.3 (0.3)	5.3 (3.5)	25.8 (12.5)	54.3 (21.5)
	TNB	3.3 (2.5)	0.4 (0.6)	2.5 (2.4)	4.9 (4.1)	35.4 (11.9)	43.8 (14.3)
	UT	1.9 (1.7)	2.7 (3.1)	0.8 (1.2)	5.1 (3.6)	24.5 (12.9)	45.8 (21.0)

		Poa pratensis 2000	*Poa pratensis* 2001	*Poa pratensis* 2002
Full	TB	5.5 (5.3)	7.6 (6.5)	8.6 (7.4)
	TNB	0.1 (0.1)	0.3 (0.4)	0.3 (0.4)
	UT	2.2 (2.0)	1.4 (1.7)	1.8 (1.4)
Part	TB	5.0 (3.3)	32.7 (20.3)	23.9 (12.1)
	TNB	2.9 (2.9)	16.1 (14.1)	18.3 (14.2)
	UT	0.6 (0.8)	8.3 (11.8)	6.0 (8.2)
None	TB	4.3 (3.5)	19.6 (17.8)	24.8 (22.3)
	TNB	0.4 (0.4)	2.7 (1.2)	5.8 (4.6)
	UT	2.0 (2.0)	18.8 (16.8)	21.7 (17.9)

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[1] Roots trenched and a plastic barrier in place. [2] Roots trenched without a barrier in place. [3] Untrenched.
[4] An admixture of *A. subsecundum, A. trachycaulum and A. dasystachyum*

Table A3-3 Trace[1] vascular plant species at Lac La Biche from 2000 to 2002.

Forbs

Achillea millefolium
Actae rubra
Equisetum arvense
Geum spp
Halenia deflexa
Mitella nuda
Pyrolia secunda
Smilacina stellata
Taraxacum officinale
Tridentalis borealis
Trifolium repens
Vicia americana
Viola adunca
Viola renifolia

Graminoids

Bromus ciliatus
Carex spp.
Poa pratensis

Tall Shrubs (>1-m tall)

Cornus stolonifera

Low Shrubs (<1-m tall)

Lonicera involucrata
Ribes spp.
Salix bebbiana

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[1] <0.5% average canopy cover throughout the experiment.

Table A3-4 Effects of aspen (*Populus tremuloides* Michx.) canopy and root trenching on canopy cover (%) of prominent vascular plant species at Lac La Biche from 2000 to 2002. Values are the arithmetic means (standard error).

Level of Canopy	Root Trenching	*Amelanchier alnifolia* (>1 m tall)			*Corylus cornuta* (>1 m tall)		
		2000	2001	2002	2000	2001	2002
Full	TB[1]	3.3 (4.7)	6.7 (9.4)	6.7 (7.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	TNB[2]	12.5 (12.1)	18.3 (16.5)	19.2 (18.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	UT[3]	1.7 (2.4)	5.2 (5.8)	7.0 (6.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Part	TB	3.3 (2.4)	0.0 (0.0)	0.8 (1.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	TNB	6.7 (5.7)	2.5 (1.6)	1.2 (1.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	UT	5.0 (3.7)	2.5 (2.4)	1.2 (1.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
None	TB	4.2 (5.9)	0.2 (0.2)	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	TNB	8.3 (6.5)	2.5 (2.4)	6.2 (5.8)	1.7 (2.4)	0.0 (0.0)	0.3 (0.5)
	UT	7.0 (6.9)	0.8 (1.2)	2.5 (3.5)	13.3 (12.5)	0.0 (0.0)	1.7 (2.4)

		Lonicera dioica (>1 m tall)			*Rosa acicularis* (>1 m tall)		
		2000	2001	2002	2000	2001	2002
Full	TB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	8.3 (5.1)	4.2 (5.9)	1.2 (1.2)
	TNB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	7.5 (4.0)	3.5 (2.4)	2.5 (1.6)
	UT	0.3 (0.5)	0.0 (0.0)	0.0 (0.0)	8.3 (5.7)	2.3 (2.4)	5.0 (5.8)
Part	TB	3.3 (4.7)	0.0 (0.0)	0.0 (0.0)	7.0 (6.9)	0.8 (1.2)	0.8 (1.2)
	TNB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	13.3 (12.5)	0.3 (0.5)	0.0 (0.0)
	UT	5.8 (6.9)	0.0 (0.0)	0.0 (0.0)	8.3 (6.5)	0.3 (0.5)	0.8 (1.2)
None	TB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	13.7 (6.7)	0.3 (0.5)	2.5 (2.4)
	TNB	0.8 (1.2)	0.0 (0.0)	0.0 (0.0)	15.8 (6.4)	0.0 (0.0)	1.2 (1.2)
	UT	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	17.5 (5.7)	5.8 (4.2)	4.2 (2.8)

Table A3-4 continued.

Level of Canopy	Root Trenching	*Salix bebbiania* (>1 m tall)			*Viburnum edule* (>1 m tall)		
		2000	**2001**	**2002**	**2000**	**2001**	**2002**
Full	TB[1]	6.7 (6.2	5.0 (4.8)	5.0 (5.8)	4.2 (4.6)	0.0 (0.0)	0.3 (0.5)
	TNB[2]	15.8 (21.0)	13.3 (18.9)	14.2 (17.4)	1.7 (1.5)	2.7 (3.8)	0.8 (1.2)
	UT[3]	1.7 (2.4)	5.2 (5.8)	4.2 (3.8)	7.5 (5.4)	0.0 (0.0)	0.8 (1.2)
Part	TB	16.7 (16.1)	2.5 (1.6)	6.7 (7.0)	5.8 (4.6)	0.0 (0.0)	0.0 (0.0)
	TNB	5.8 (6.9)	0.0 (0.0)	1.7 (1.5)	1.7 (2.4)	0.0 (0.0)	0.0 (0.0)
	UT	15.8 (17.4)	16.7 (17.5)	18.3 (18.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
None	TB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.7 (1.5)	0.0 (0.0)	0.0 (0.0)
	TNB	8.3 (11.8)	0.0 (0.0)	0.8 (1.2)	1.7 (2.4)	0.0 (0.0)	0.0 (0.0)
	UT	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
		Amelanchier alnifolia (<1 m tall)			*Cornus stolonifera* (<1 m tall)		
		2000	**2001**	**2002**	**2000**	**2001**	**2002**
Full	TB	0.0 (0.0)	0.0 (0.0)	0.8 (1.2)	0.0 (0.0)	0.2 (0.2)	0.0 (0.0)
	TNB	0.0 (0.0)	0.0 (0.0)	1.7 (2.4)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	UT	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Part	TB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	TNB	0.0 (0.0)	0.3 (0.5)	0.4 (0.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	UT	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.2)	0.0 (0.0)
None	TB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.3 (1.8)	1.2 (1.2)	4.8 (4.3)
	TNB	0.0 (0.0)	5.0 (7.1)	5.0 (5.8)	2.5 (3.5)	1.2 (1.2)	3.1 (4.4)
	UT	0.0 (0.0)	1.0 (1.4)	5.0 (7.1)	0.0 (0.0)	8.2 (9.1)	4.6 (3.7)

Table A3-4 continued.

Level of Canopy	Root Trenching	*Linnaea borealis* (<1 m tall) 2000	2001	2002	*Lonicera dioica* (>1 m tall) 2000	2001	2002
Full	TB[1]	0.4 (0.6)	0.0 (0.0)	0.0 (0.0)	0.2 (0.2)	0.0 (0.0)	0.4 (0.6)
	TNB[2]	0.0 (0.0)	0.2 (0.2)	0.0 (0.0)	1.3 (1.8)	10.8 (15.3)	0.4 (0.6)
	UT[3]	0.1 (0.1)	1.2 (1.6)	1.7 (2.4)	2.3 (2.5)	2.8 (2.8)	2.1 (2.3)
Part	TB	1.3 (1.3)	0.2 (0.2)	0.8 (1.2)	5.3 (5.6)	0.0 (0.0)	0.0 (0.0)
	TNB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.4 (0.6)	0.0 (0.0)	2.1 (2.9)
	UT	0.5 (0.6)	0.2 (0.2)	0.8 (1.1)	6.0 (8.2)	0.0 (0.0)	1.7 (2.4)
None	TB	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	7.5 (5.8)	1.2 (1.6)	3.8 (4.1)
	TNB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	6.7 (9.4)	0.8 (1.2)	3.1 (3.2)
	UT	0.0 (0.0)	10.8 (15.3)	0.0 (0.0)	6.8 (5.9)	2.3 (2.2)	1.7 (1.7)
		***Rosa acicularis* (<1 m tall)**			***Rubus idaeus* (<1 m tall)**		
		2000	**2001**	**2002**	**2000**	**2001**	**2002**
Full	TB	13.2 (7.8)	13.0 (6.4)	8.7 (3.1)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
	TNB	7.3 (3.5)	18.1 (6.5)	17.4 (7.2)	0.0 (0.0)	0.3 (0.5)	0.0 (0.0)
	UT	6.4 (3.4)	7.9 (3.5)	9.7 (3.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Part	TB	11.4 (7.7)	14.9 (9.3)	12.7 (8.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	TNB	10.8 (6.9)	8.8 (4.6)	11.6 (3.4)	0.0 (0.0)	0.2 (0.2)	0.0 (0.0)
	UT	10.7 (8.4)	12.8 (6.1)	10.8 (5.8)	0.0 (0.0)	0.0 (0.0)	5.0 (7.1)
None	TB	18.0 (9.2)	16.4 (10.1)	13.1 (5.5)	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)
	TNB	11.3 (9.3)	21.4 (8.9)	21.2 (5.0)	1.0 (1.4)	0.0 (0.0)	0.0 (0.0)
	UT	5.3 (2.6)	17.6 (9.4)	26.0 (9.4)	3.9 (3.7)	0.7 (0.9)	2.1 (2.9)

Table A3-4 continued.

Level of Canopy	Root Trenching	*Symphoricarpos albus* (<1 m tall) 2000	2001	2002	*Vibernum edule* (>1 m tall) 2000	2001	2002
Full	TB^1	3.8 (2.9)	3.7 (2.0)	6.5 (2.7)	5.0 (4.0)	2.8 (2.8)	7.7 (6.9)
	TNB^2	4.3 (4.6)	2.8 (2.4)	2.4 (1.9)	9.4 (8.1)	24.0 (11.6)	29.3 (14.1)
	UT^3	0.9 (0.7)	1.3 (1.0)	1.9 (1.3)	9.3 (7.0)	9.8 (4.6)	11.2 (5.9)
Part	TB	4.1 (3.9)	9.3 (4.7)	11.6 (5.3)	7.7 (5.4)	2.7 (3.5)	9.5 (11.5)
	TNB	7.5 (4.6)	5.0 (4.5)	13.3 (9.5)	5.8 (2.8)	3.9 (3.4)	5.0 (2.6)
	UT	1.0 (0.7)	2.9 (1.5)	7.5 (2.2)	4.8 (3.1)	7.1 (4.7)	13.3 (8.6)
None	TB	3.8 (3.6)	9.8 (6.3)	14.2 (6.5)	1.6 (1.5)	8.9 (5.7)	12.7 (7.6)
	TNB	10.8 (8.1)	3.1 (2.2)	13.3 (11.4)	9.2 (6.7)	6.0 (4.9)	6.3 (5.4)
	UT	2.1 (1.9)	4.1 (3.3)	2.0 (1.3)	2.8 (3.5)	2.7 (2.5)	5.2 (5.1)
		Aralia nudicaulis			***Aster ciliolatus***		
		2000	**2001**	**2002**	**2000**	**2001**	**2002**
Full	TB	0.4 (0.6)	0.0 (0.0)	0.0 (0.0)	0.3 (0.2)	3.7 (2.1)	2.9 (2.0)
	TNB	0.0 (0.0)	0.2 (0.2)	0.0 (0.0)	1.1 (1.1)	5.0 (3.4)	3.1 (2.0)
	UT	0.1 (0.1)	1.2 (1.6)	1.7 (2.4)	0.4 (0.3)	6.3 (3.3)	7.9 (2.8)
Part	TB	1.3 (1.3)	0.2 (0.2)	0.8 (1.2)	1.8 (1.1)	1.9 (1.0)	4.2 (3.0)
	TNB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (0.6)	5.3 (4.4)	5.8 (6.4)
	UT	0.5 (0.6)	0.2 (0.2)	0.8 (1.1)	0.4 (0.6)	1.7 (0.8)	3.1 (1.8)
None	TB	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	1.7 (1.7)	2.0 (1.2)	3.7 (2.0)
	TNB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.2)	0.8 (0.7)	1.0 (1.4)
	UT	0.0 (0.0)	10.8 (15.3)	0.0 (0.0)	0.0 (0.0)	1.7 (2.1)	1.4 (2.0)

Table A3-4 continued.

Level of Canopy	Root Trenching	*Aster conspicuous*			*Cornus canadensis*		
		2000	**2001**	**2002**	**2000**	**2001**	**2002**
Full	TB[1]	1.4 (1.3)	1.3 (1.6)	4.1 (3.9)	1.7 (0.8)	1.2 (0.6)	4.2 (3.4)
	TNB[2]	3.0 (2.1)	3.6 (2.8)	3.1 (2.5)	1.8 (1.2)	1.7 (1.6)	3.3 (2.2)
	UT[3]	1.1 (1.3)	2.0 (1.8)	1.0 (0.7)	1.4 (0.8)	1.7 (0.8)	3.2 (1.1)
Part	TB	1.1 (1.3)	1.2 (0.8)	10.8 (5.7)	1.3 (0.7)	1.1 (0.7)	3.1 (2.6)
	TNB	2.7 (2.2)	3.2 (3.2)	15.2 (7.2)	0.9 (0.9)	0.7 (0.7)	1.2 (0.7)
	UT	3.8 (4.0)	2.2 (1.3)	7.3 (3.9)	2.2 (1.3)	0.8 (0.7)	2.3 (1.3)
None	TB	0.0 (0.0)	0.5 (0.5)	1.3 (1.2)	0.1 (0.1)	0.8 (0.6)	2.0 (1.4)
	TNB	0.3 (0.2)	0.8 (0.9)	5.4 (4.0)	0.8 (0.6)	0.8 (0.5)	0.9 (0.9)
	UT	0.6 (0.6)	4.3 (3.3)	4.3 (2.7)	0.6 (0.6)	0.9 (1.2)	2.1 (1.7)
		Epilobium angustifolium			*Fragaria virginiana*		
		2000	**2001**	**2002**	**2000**	**2001**	**2002**
Full	TB	3.2 (1.6)	1.6 (1.6)	2.8 (3.1)	0.7 (0.3)	2.2 (1.3)	3.8 (2.8)
	TNB	2.3 (2.9)	1.8 (2.6)	3.9 (2.8)	1.8 (0.8)	2.1 (1.5)	3.8 (2.1)
	UT	3.3 (1.9)	1.7 (1.3)	1.3 (1.0)	1.4 (1.2)	1.1 (0.8)	0.3 (0.3)
Part	TB	5.4 (6.3)	1.4 (0.9)	8.3 (5.6)	1.6 (0.8)	2.7 (2.3)	9.6 (7.3)
	TNB	6.2 (4.8)	3.8 (3.4)	9.2 (6.2)	0.4 (0.4)	0.2 (0.2)	2.9 (3.5)
	UT	1.8 (0.7)	4.5 (2.5)	4.9 (2.1)	1.6 (1.4)	1.5 (1.4)	5.0 (5.2)
None	TB	1.3 (1.8)	1.3 (0.8)	4.0 (1.5)	0.2 (0.2)	0.0 (0.0)	0.2 (0.2)
	TNB	5.1 (3.7)	2.8 (1.2)	5.8 (1.9)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	UT	2.8 (2.3)	3.5 (2.6)	9.3 (2.2)	0.8 (1.2)	0.0 (0.0)	0.2 (0.2)

Table A3-4 continued.

Level of Canopy	Root Trenching	*Galium boreale*			*Lathyrus ochroleucus*		
		2000	2001	2002	2000	2001	2002
Full	TB[1]	2.8 (1.2)	3.8 (0.6)	5.0 (1.6)	0.2 (0.2)	0.3 (0.2)	0.3 (0.3)
	TNB[2]	1.8 (1.1)	1.0 (0.5)	1.6 (0.7)	1.0 (0.7)	0.4 (0.3)	0.4 (0.6)
	UT[3]	1.9 (0.6)	2.4 (1.4)	2.1 (0.5)	0.2 (0.2)	0.3 (0.5)	0.0 (0.0)
Part	TB	1.3 (0.8)	1.8 (1.1)	6.6 (3.1)	0.0 (0.0)	0.9 (0.6)	0.2 (0.2)
	TNB	1.7 (0.8)	3.6 (3.2)	7.8 (2.9)	1.3 (0.9)	1.3 (1.2)	0.9 (0.6)
	UT	1.1 (0.6)	1.3 (1.2)	5.3 (2.2)	1.2 (1.2)	1.1 (1.1)	1.3 (1.2)
None	TB	1.9 (0.6)	2.6 (0.8)	4.0 (1.8)	0.3 (0.3)	0.9 (0.6)	1.6 (1.1)
	TNB	1.3 (0.7)	1.9 (0.7)	3.6 (1.4)	0.5 (0.5)	2.4 (2.6)	3.5 (4.0)
	UT	1.0 (0.5)	1.8 (1.7)	1.8 (0.8)	0.6 (0.6)	0.7 (0.7)	0.8 (0.6)
		Maiantherum canadensis			*Petasites palmatus*		
		2000	2001	2002	2000	2001	2002
Full	TB	1.2 (0.4)	1.3 (0.8)	1.6 (1.7)	0.2 (0.2)	0.7 (0.9)	0.6 (0.8)
	TNB	1.4 (1.1)	1.0 (0.9)	1.3 (0.8)	0.1 (0.1)	0.3 (0.2)	0.2 (0.2)
	UT	0.8 (0.6)	1.9 (1.0)	0.9 (0.8)	0.3 (0.3)	0.3 (0.2)	0.8 (0.7)
Part	TB	0.8 (0.5)	0.5 (0.4)	2.4 (1.4)	1.1 (0.6)	0.2 (0.1)	4.3 (3.6)
	TNB	0.2 (0.1)	0.2 (0.1)	1.1 (0.8)	0.5 (0.7)	1.5 (1.9)	5.6 (3.4)
	UT	1.3 (0.9)	0.7 (0.3)	1.6 (1.2)	2.2 (2.9)	1.3 (1.2)	0.6 (0.8)
None	TB	1.8 (1.3)	1.8 (0.6)	2.7 (1.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.2)
	TNB	1.5 (0.5)	1.5 (0.8)	2.8 (1.0)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)
	UT	0.6 (0.6)	1.8 (0.7)	1.5 (0.8)	0.1 (0.1)	0.2 (0.2)	0.0 (0.0)

Table A3-4 continued.

Level of Canopy	Root Trenching	*Rubus pubescens* 2000	*Rubus pubescens* 2001	*Rubus pubescens* 2002	*Calamagrostis canadensis* 2000	*Calamagrostis canadensis* 2001	*Calamagrostis canadensis* 2002
Full	TB[1]	1.6 (1.7)	2.0 (1.4)	8.1 (5.3)	0.7 (0.2)	0.4 (0.3)	1.3 (0.5)
	TNB[2]	1.3 (1.2)	1.0 (0.7)	0.8 (1.2)	0.7 (0.6)	0.3 (0.2)	0.8 (0.6)
	UT[3]	0.2 (0.2)	0.7 (0.3)	3.0 (2.7)	0.7 (0.2)	0.4 (0.5)	0.5 (0.3)
Part	TB	1.7 (2.4)	1.3 (1.0)	6.3 (4.6)	0.5 (0.6)	0.3 (0.2)	2.0 (1.7)
	TNB	1.0 (1.2)	0.3 (0.5)	6.0 (4.6)	0.3 (0.4)	0.2 (0.2)	1.0 (0.9)
	UT	1.3 (1.8)	0.7 (0.9)	2.4 (3.1)	0.6 (0.3)	0.3 (0.4)	1.4 (0.9)
None	TB	1.1 (0.8)	15.4 (10.5)	12.7 (8.8)	0.3 (0.2)	0.1 (0.1)	1.4 (1.3)
	TNB	1.0 (0.9)	2.8 (3.3)	3.9 (3.4)	0.3 (0.3)	0.1 (0.1)	0.7 (0.3)
	UT	1.4 (1.4)	2.7 (2.6)	2.9 (2.6)	0.1 (0.1)	0.0 (0.0)	0.3 (0.3)

		Elymus innovatus 2000	*Elymus innovatus* 2001	*Elymus innovatus* 2002
Full	TB	0.0 (0.0)	0.3 (0.4)	0.0 (0.0)
	TNB	0.0 (0.0)	0.2 (0.1)	1.0 (0.9)
	UT	0.0 (0.0)	0.3 (0.2)	2.1 (2.9)
Part	TB	0.0 (0.0)	0.5 (0.7)	5.2 (5.2)
	TNB	0.0 (0.0)	0.0 (0.0)	1.0 (1.2)
	UT	0.0 (0.0)	0.6 (0.6)	1.4 (1.7)
None	TB	0.0 (0.0)	0.0 (0.0)	0.4 (0.6)
	TNB	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	UT	0.0 (0.0)	2.8 (3.9)	0.0 (0.0)

[1] Roots trenched and a plastic barrier in place. [2] Roots trenched without a barrier in place. [3] Untrenched.

APPENDIX 4

Leaf-to-Atmosphere Vapour Pressure Difference Calculations

Leaf-to-atmosphere vapour pressure difference (D) calculations, corrected (Jones 1992) for the conversion of the saturated pressure of pure water vapour to the saturation partial pressure of water vapour in moist air:

(1) $D = e_L - e_A$

D = Leaf-to-atmosphere vapour pressure difference (kPa)
e_L = Leaf mesophyll vapour pressure
e_A = Atmospheric vapour pressure

(2) $e_A = RH * e_s(T_a)$

RH = Relative humidity (%)

(3) $e_s(T_a) = a \exp\left\{\frac{bT_a}{c + T_a}\right\}$

a = 0.61375
b = 17.502
c = 240.97
T_a = air temperature in °C

(4) $e_L = e_s(T_L)^{\#}$

(5) $e_s(T_L) = a \exp\left\{\frac{bT_L}{c + T_L}\right\}$

a = 0.61375
b = 17.502
c = 240.97
T_L = leaf temperature in °C

[#] Air in the leaf mesophyll is assumed to be at saturation (100% RH).

Literature Cited

Jones, H.G. 1992. Plants and Microclimate, A Quantitative Approach to Environmental Plant Physiology. 2nd Edition, Cambridge University Press, Cambridge, UK, p 110, 359.